

Climate-driven shifts in the distribution of the rare earth element hyperaccumulator fern *Blechnopsis orientalis*: Implications for phytomining and conservation strategies in China

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ABSTRACT

Rising global temperatures are altering species distributions, yet the long-term dynamics of pteridophytes remain poorly documented. Here, we project the potential habitat dynamics of *Blechnopsis orientalis*, a fern with exceptional rare earth element (REE) accumulation capacity and promising applications in green phytomining, across China under both contemporary and future climate scenarios. Using 646 valid occurrence records and ten comprehensively selected environmental predictors, we applied a parameter-optimized MaxEnt model ($RM = 1$, $FC = QHPT$, $AUC = 0.947$) to evaluate habitat suitability. For future trend simulation, four representative CMIP6 scenarios (SSP126, SSP245, SSP370, and SSP585) were selected, and predictions were analyzed for three time slices (2050s, 2070s, and 2090s). Our principal findings are: (1) Bio9 (Mean Temperature of Driest Quarter) and Bio12 (Annual Precipitation) are the primary drivers of the species' distribution, with a cumulative contribution of 86.7%, confirming temperature and water availability as core limiting factors. (2) Contrary to the widely observed range contraction in most rare plants, *B. orientalis* exhibits a significant net expansion under all climate scenarios, with the maximum projected expansion area reaching $59.64 \times 10^4 \text{ km}^2$, while the contracted area remains below $0.83 \times 10^4 \text{ km}^2$. (3) The centroid of suitable habitat shifts generally northwestward, with displacement distances increasing with scenario severity and reaching up to 108.75 km under SSP585-2090s. These findings indicate that *B. orientalis* possesses strong adaptive capacity to climate warming, and its rare-earth hyperaccumulation function may impose additional constraints on its climatic niche through a transpiration-dependent mechanism. Based on these comprehensive results, we propose three systematic conservation and development schemes: (i) prioritizing the interconnected provincial border zones in southwestern South China as core functional areas for in situ conservation of wild populations; (ii) developing the inland interprovincial junction zone in eastern South China into an official pilot site for the application and dissemination of rare-earth phytomining technology; and (iii) establishing specialized germplasm preservation bases along the axis of the population centroid shift.

1. Introduction

Climate warming is driving thousands of plant species globally toward higher latitudes and higher elevations, yet the rates and directions of these responses vary significantly among different taxonomic groups and regions (Lenoir et al., 2020; Steinbauer et al., 2018). Ferns, as the

second-largest group of vascular plants after angiosperms, possess strong spore dispersal capabilities and are therefore considered more likely than most seed plants to achieve equilibrium with climate (Qian et al., 2023). At the same time, their gametophyte stage lacks cuticular protection and is highly sensitive to water and temperature stress (Blake-Mahmud et al., 2025; Krieg and Chambers, 2022). These unique

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reproductive and biological characteristics suggest that ferns may respond to climate change through mechanisms different from those of seed plants (Brodrribb and McAdam, 2011). However, compared with angiosperms, studies predicting the distributional dynamics of ferns remain severely limited, and this knowledge asymmetry is constraining our comprehensive assessment of conservation priorities for plant diversity under global change (Michael and Jürgen, 2022). In East Asia, where fern diversity is exceptionally high (Qian et al., 2026), systematic distribution modeling studies focusing on endemic or near-endemic ferns in this region under global climate change are still very limited.

Blechnopsis orientalis (L.) C. Presl (*B. orientalis*) is broadly distributed across tropical and subtropical Asia (Huang et al., 2025), with continuous occurrence records throughout southern China where it commonly inhabits evergreen broad-leaved forests. Beyond its ecological and medicinal values, groundbreaking studies have revealed that *B. orientalis* is a rare earth element (REE) hyperaccumulator, with REE concentrations in its tissues reaching as high as $1735\text{--}3850\text{ }\mu\text{g g}^{-1}$ (Corzo-Remigio et al., 2026; He et al., 2025; Purwadi et al., 2025). Furthermore, it can form high-value nanoscale monazite minerals through plant-mediated mineralization processes under ambient temperature and pressure. This characteristic positions *B. orientalis* as a promising species for green phytomining (Han et al., 2025; Huang et al., 2026; Liu et al., 2025a; van der Ent et al., 2026), with substantial potential for sustainable REE supply and green synthesis of functional nanomaterials. However, current research on this species is highly concentrated on its physiology, biochemistry, and pharmacological activities (Dong et al., 2024; Jiang et al., 2022; Waswa et al., 2022). However, a critical question that will determine the species' prospects for ecological remediation and resource application remains entirely unaddressed by quantitative assessment: how is the geographic distribution of *B. orientalis* controlled by climate, and how will future climate change reshape its suitable habitat?

Three interconnected methodological and conceptual limitations characterize the existing literature. First, with respect to species distribution modeling, no previous investigation has addressed the potential geographic range of *B. orientalis* across China. Although Dicranopteris species (*D. linearis* and *D. pedata*) produce greater biomass and are the most intensively studied REE hyperaccumulator ferns in southern China, *B. orientalis* is distinguished by the deposition of REE as nanoscale monazite (He et al., 2025), a mineral form that may facilitate downstream REE recovery. Available studies primarily emphasize phytochemistry, pharmacological activities, and localized community surveys (Gao et al., 2022; Mala et al., 2022; Wan et al., 2026), without integrating occurrence data with environmental predictors to quantitatively identify the climatic determinants of its geographic boundaries. Second, at the methodological level, existing distribution modeling studies on ferns commonly lack parameter optimization (Wang et al., 2016; Wei et al., 2021). The default MaxEnt parameterization comprises a regularization multiplier (RM) of 1 and LQHP feature combinations (FC). This setup easily causes overfitting on high-dimensional environmental datasets with limited samples and generates systematic biases in predicted probabilities (Morales et al., 2017; Muscarella et al., 2014). Models without optimization usually overrate the degree of habitat fragmentation and downplay the elasticity of species responding to climate changes (Radosavljevic and Anderson, 2014). Third, there is still a lack of systematic climatic predictions for Chinese subtropical fern species that adopt the multi-scenario and multi-period analytical framework from the CMIP6 model set (Wang et al., 2024).

Drawing upon the biological attributes of *B. orientalis* and its distinctive REE hyperaccumulation capability, we propose three hypotheses: (H1) Of all environmental factors shaping the distribution of *B. orientalis*, temperature and moisture exert the primary controls. This dominant driving mechanism is tightly linked to transpiration and phosphate precipitation, two processes enabling efficient rare earth

element enrichment; (H2) Future climate warming will drive the centroid of suitable habitat for *B. orientalis* toward higher latitudes and higher elevations; (H3) Since extant populations have not yet hit their maximum thermal threshold, and their distinctive mineralization pathways grant enhanced climatic resilience, warming will drive a net increase in potentially suitable habitat. In order to verify the above hypotheses, the present study adopted an optimized MaxEnt model combined with multi-source distribution records and high-resolution environmental factors. Furthermore, the CMIP6 prediction system covering diverse climate scenarios and different time periods was applied to comprehensively explore the distribution patterns of potentially suitable habitats as well as their spatial dynamic migration traits of *B. orientalis* under present and forthcoming climatic conditions. By integrating explicit a priori hypotheses, rigorous model optimization, and multi-scenario predictions, this study aims to reveal the response characteristics of REE hyperaccumulator plants to climate change and to provide a testable and reproducible methodological reference for assessing the climate vulnerability of other medicinal and resource-valued ferns in East Asia. The findings can assist in screening key habitats for the in-situ conservation of *B. orientalis*, offer references for selecting reasonable locations of REE phytomining projects under changing climatic conditions, and furnish theoretical and data basis for the development of ex-situ conservation schemes as well as sustainable collection strategies of this plant species.

2. Materials and methods

2.1. Occurrence data collection and preprocessing

Distribution records of *B. orientalis* across China were collated from open-access online repositories and published literatures. The main data platforms covered the Chinese Virtual Herbarium (CVH; website: <http://www.cvh.ac.cn/>, retrieval date: 25 November 2025), the Global Biodiversity Information Facility (GBIF; <https://doi.org/10.15468/dl.rngjzg>, retrieval date: 26 November 2025), China National Knowledge Infrastructure (CNKI; <https://www.cnki.net/>, retrieval date: 26 November 2025), as well as Google Scholar (<https://ac.scmor.com/>, retrieval date: 27 November 2025). Some specimen entries contained precise collection locations ranging from county and township to village levels yet lacked corresponding precise latitude and longitude values. For such records, the coordinate query website Jingweidu Query Positioning Tool (<http://jingweidu.757dy.com/>, accessed 27 May 2025) was adopted to supplement missing geographic coordinate data. Redundant duplicate records were eliminated via the duplicate deletion tool embedded in Microsoft Excel 2016. After deduplication, a raw dataset containing 2525 presence points was acquired, among which 2394 records derived from GBIF, 102 from CVH, 22 from CNKI and 7 from Google Scholar. To alleviate sampling unevenness and eliminate spatial aggregation bias of distribution points, a grid with a resolution of $2.5'\times 2.5'$ was created in ArcGIS 10.8 software. For each individual grid unit, only the occurrence point closest to the grid centroid was preserved. After this spatial thinning procedure, the dataset was optimized to contain 646 valid distribution records, including 535 GBIF entries, 89 CVH entries, 16 CNKI entries, and 6 Google Scholar entries. This cleaned dataset served as the fundamental material for subsequent niche modeling analyses (Fig. 1). All processed occurrence data were organized and exported as CSV files to match the input format criteria of MaxEnt 3.4.4 modeling software (http://biodiversityinformatics.amnh.org/open_source/maxent/, accessed 27 November 2025). The geographic mapping in this research adopted the official standard China base map issued by the Standard Map Service Platform under the Ministry of Natural Resources of China, with the drawing approval number GS (2023)2762. This standard map resource was downloaded from the official platform (<http://bzdt.ch.mnr.gov.cn/>) on 22 December 2023.

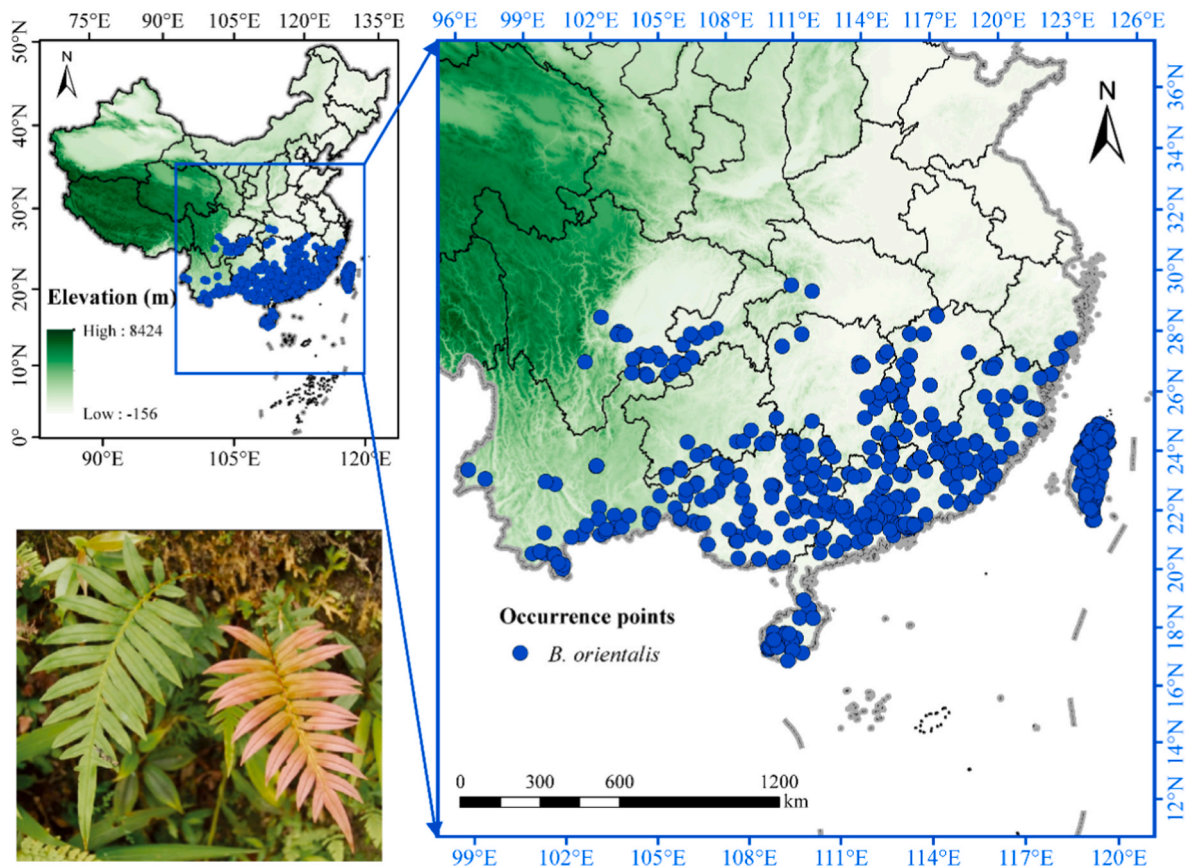


Fig. 1. Distribution records of *B. orientalis* across China. Photo of *B. orientalis* originated from Zhu et al. (2013).

2.2. Preprocessing of environmental variable datasets

This study adopted four groups of environmental drivers (climate, topography, vegetation and human interference) to simulate the distribution pattern of *B. orientalis*, and 24 candidate variables were initially retained (Table S1). We downloaded 19 bioclimatic variables (Booth et al., 2014) and elevation information from WorldClim 2.1 (<https://www.worldclim.org/>, accessed 8 November 2025). Terrain metrics of slope and aspect were generated based on elevation data in ArcGIS 10.8. MODIS/Terra MOD13A3 NDVI datasets (Didan, 2015) served as the proxy for vegetation conditions, and the Human Footprint Index (Venter et al., 2016) was utilized to measure human activity levels.

A standardized workflow was adopted to eliminate multicollinearity between environmental and topographic variables in this study. Firstly, attribute data of all variables were extracted from 646 distribution sites using the Extract Multi Values to Points function embedded in ArcGIS 10.8 software. Subsequently, Spearman correlation analysis was conducted in Origin 2026 to quantify the correlation degree between every pair of variables (Fig. 2). Two screening principles referring to previous research were adopted to filter highly correlated variables: (1) all variables with an absolute correlation coefficient ($|r|$) lower than 0.7 were reserved for subsequent modelling (Dormann et al., 2013); (2) for variable combinations with $|r| \geq 0.7$, only the variable with higher explanatory power in the preliminary MaxEnt model was retained, and the detailed screening results are summarized in Table S1. To obtain the contribution rate of each predictor variable, a preliminary MaxEnt model containing all 24 original variables was constructed, and the jackknife test was adopted to evaluate the independent contribution of each variable. Ultimately, 10 independent predictor variables with low collinearity were screened out to build the final species distribution model, including Isothermality (Bio3), Maximum temperature of

warmest month (Bio5), Mean temperature of wettest quarter (Bio8), Mean temperature of driest quarter (Bio9), Annual precipitation (Bio12), Precipitation of driest quarter (Bio17), Slope, Aspect, normalized difference vegetation index (NDVI) and human footprint index (HFI). Soil type was not included for two reasons. First, macroscale SDM studies consistently show that soil variables contribute little explanatory power compared with climatic factors. Second, available large-scale soil datasets for China have coarse resolution and limited accuracy, potentially introducing more uncertainty than explanatory power.

The present research adopted the BCC-CSM2-MR global climate model, whose capability to accurately reconstruct China's regional climate regimes has been fully validated in the research of Lu et al. (2025), so as to explore the shifts in the geographical distribution of *B. orientalis* triggered by climatic changes. Projections of habitat distribution variations were generated for three distinct future periods corresponding to the middle, later and final stages of the 21st century, i.e., the 2050s (2041–2060), 2070s (2061–2080) and 2090s (2081–2100), with simulations conducted under four Shared Socioeconomic Pathway scenarios including SSP126, SSP245, SSP370 and SSP585. According to Fan et al. (2024), the four pathways will maintain steady radiative forcing magnitudes of 2.6, 4.5, 7.0 and 8.5 W/m² up to 2100.

2.3. Model tuning and spatial forecasting of the MaxEnt model

2.3.1. Model calibration of the MaxEnt model

Unoptimized model parameters can lead to systematic bias in predicted probabilities, causing the predicted potential distribution of a species to deviate from its actual pattern (Guisan and Thuiller, 2005), thereby either overestimating or underestimating the suitable habitat range of *B. orientalis*. To resolve this problem, we tuned all relevant parameters with the ENMevaluate function developed by Kass et al.

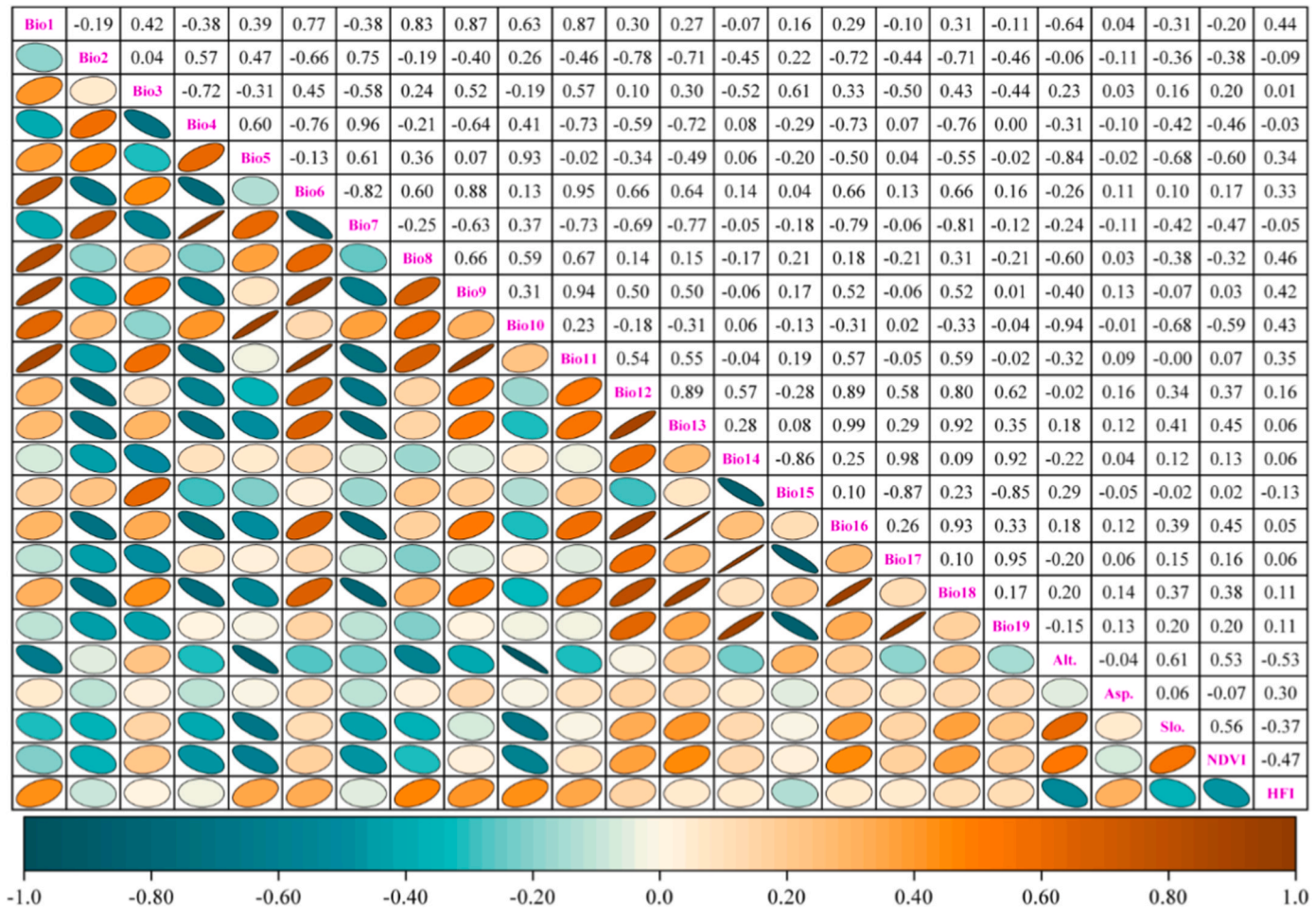


Fig. 2. Spearman correlation matrix revealing pairwise linkages between the 24 environmental variables. Ellipse elongation denotes the magnitude of correlation, where highly elongated shapes equate to greater absolute correlation coefficients. Correlation polarity is distinguished by color depth: darker cyan signals stronger negative correlations, and deeper brown indicates more pronounced positive correlations.

(2021) in ENMeval version 2.0.4, under R 4.2.2 environment. Specifically, the regularization multiplier (RM) ranging from 0.5 to 4.0 with a step size of 0.5 was paired with five feature classes (L: linear, Q: quadratic, P: product, T: threshold, H: hinge), generating nine candidate feature sets (Muscarella et al., 2014). To determine the optimal parameter combination, we evaluated both model fit and complexity using delta AICc alongside 10% Training Omission Rate (OR10) (Phillips et al., 2017). This optimization procedure was essential for producing reliable assessments of how future climate scenarios are likely to reshape the geographic range of *B. orientalis*.

2.3.2. Parameter configuration of the MaxEnt model

This study adopted a MaxEnt modelling framework with balanced prediction accuracy and robustness to explore the distribution characteristics of potentially suitable habitats for *Bufo orientalis* amid ongoing climate change. A total of 646 distribution records with strict quality screening were adopted as the fundamental dataset for model construction. In the first step, stratified random sampling was applied to divide the original occurrence data into two subsets: a training dataset accounting for 75% of all records (485 samples) and an independent validation dataset occupying the remaining 25% (161 samples). This data splitting method guaranteed that both subsets could fully reflect the overall environmental characteristics of the study area, while eliminating statistical correlation between model training and model

assessment processes. In accordance with standard specifications for ecological niche modelling, multiple parameter optimization measures were implemented to improve model performance. Specifically, cross-validation was adopted to optimize the internal verification effect of the model; 10000 background points were configured to comprehensively reflect the heterogeneous features of regional environmental backgrounds. The regularization multiplier was fixed at 1 to effectively prevent model overfitting, and the QHPT feature combination was chosen to precisely fit the intricate non-linear relationships between the survival of *Bufo orientalis* and diverse environmental variables. To minimize random errors generated during model operation, the simulation was repeated ten times, and the average value of all simulation results was taken as the final modelling outcome. Ultimately, logistic raster files in .asc format containing habitat suitability probability values were exported, laying a solid data foundation for follow-up spatial statistics, comparative analysis across multiple climate scenarios and result visualization.

2.3.3. Accuracy assessment for predictions of the optimized model

In this study, three common evaluation indicators, including the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), and Cohen's kappa coefficient (Kappa), were adopted to comprehensively assess the predictive performance of the MaxEnt model (Li et al., 2026). As a classic evaluation metric, AUC quantifies the

model's ability to discriminate between species occurrence records and randomly selected background points. Its values range from 0.5 to 1.0. Specifically, AUC values of 0.5–0.6 indicate ineffective predictions; 0.6–0.7 reflects low predictive accuracy; 0.7–0.8 denotes moderate performance; 0.8–0.9 represents high accuracy; and values above 0.9 suggest outstanding predictive capability (Xue et al., 2026). Unlike AUC, TSS accounts for both sensitivity and specificity, thereby correcting for biases arising from unbalanced sample sizes. The interpretation criteria for TSS are as follows: values below 0.4 indicate poor performance; 0.4–0.5 denotes moderate; 0.5–0.7 indicates good; 0.7–0.85 represents very good; 0.85–0.9 signifies excellent; and 0.9–1.0 reflects nearly perfect predictive performance (Bai et al., 2024). The Kappa coefficient assesses the agreement between model predictions and observed distribution data while accounting for chance agreement. Kappa values below 0.4 indicate poor agreement between predictions and observations; values of 0.4–0.75 reflect substantial agreement; and values above 0.75 indicate excellent agreement (Li et al., 2019).

2.4. Division of habitat areas by suitability

To delineate ecologically meaningful habitat boundaries, we applied a two-step classification workflow to the continuous MaxEnt suitability raster. First, we binarized the study area into suitable and non-suitable habitats using the 10th percentile training presence threshold (Radosavljevic and Anderson, 2014). This threshold allows the model to omit 10% of training presence points (i.e., controls the false negative rate), effectively excluding marginal records that may arise from geo-coordinate errors, local microhabitat anomalies, or sampling bias, thereby balancing the overprediction associated with the minimum presence threshold and the arbitrariness of fixed probability thresholds. To reduce uncertainty from single runs, we calculated the arithmetic mean of thresholds from 10 repeated runs (0.0994) as the uniform binarization standard. To further explore the quality heterogeneity within the identified suitable habitats, the corresponding raster values were exported to ArcGIS 10.8 for unsupervised classification using the Natural Breaks (Jenks) algorithm (Liu et al., 2025b). Through iterative optimization, this approach enhances internal cohesion while maximizing separation between classes, enabling the objective identification of inherent thresholds in the suitability probability distribution. The potential suitable habitat of *B. orientalis* was finally partitioned into four suitability levels: unsuitable (≤ 0.0994), low (0.0994–0.3), medium (0.3–0.5), and high (> 0.5). This four-tier classification integrated the Natural Breaks-generated thresholds with ecological considerations to ensure biological meaningfulness. By adopting this categorization approach, researchers can substantially boost the differentiation degree of spatial distribution features across appropriate living environments.

2.5. Spatial variation of suitable habitat distribution

To assess climate-driven habitat dynamics of *B. orientalis* across scenarios and time periods, we classified suitable areas into three spatiotemporal categories: stable (suitable now and future), shrunk (suitable now only), and expanded (future only). This scheme enables standardized quantification of distributional responses and provides a theoretical basis for conservation prioritization. The workflow involved: (i) importing baseline and future (2050s, 2070s, 2090s) suitability rasters under four SSPs (126, 245, 370, 585) into ArcGIS 10.8; (ii) binarizing each raster at the 0.0994 threshold; (iii) classifying transitions ($1 \rightarrow 1$ = stable, $1 \rightarrow 0$ = shrunk, $0 \rightarrow 1$ = expanded); (iv) converting rasters to vector polygons; and (v) performing overlay analysis via the Intersect tool to produce scenario-specific distribution maps.

2.6. Centroid transfer of habitat suitability zones

To track the spatial displacement of *B. orientalis* habitats under climate change, we extracted habitat centroids using ArcGIS 10.8 and

calculated their migration distances across time periods. The analysis covered a baseline (1970–2000) and three future windows (2050s, 2070s, 2090s) under SSP126, SSP370, and SSP585. Our workflow involved three steps: (i) converting MaxEnt-derived suitability rasters into binary vectors at the 0.0994 threshold; (ii) computing centroid coordinates for suitable habitat polygons via ArcGIS's geometric analysis tool; and (iii) calculating Euclidean distances to determine net centroid displacement, providing insights into the directional shifts of suitable habitats under projected climate scenarios.

3. Results

3.1. Optimization and precision assessment of the MaxEnt model

Under the default parameter configuration (FC = LQHP and RM = 1), the delta AICc value was 68.32, substantially exceeding the critical threshold of 2 recommended by Anderson and Gonzalez (2011), indicating marked underfitting. Such default settings failed to adequately capture the complex relationships between species distribution and key environmental drivers. Based on 646 validated occurrence records of *B. orientalis* and 10 major environmental predictors, the ENMeval R package was applied for parameter optimization. Two alternative schemes satisfying delta AICc < 2 were identified: RM = 1 with FC = QHPT (delta AICc = 0) and RM = 1 with FC = LQHPT (delta AICc = 1.76) (Fig. 3a). Given their comparable statistical performance, the OR10 index was further adopted to evaluate model stability and conservative predictive capacity. The results showed that the optimized combination (RM = 1, FC = QHPT) yielded an OR10 of 0.2950, slightly lower than the default model's 0.2966, representing a 0.53% reduction (Fig. 3b). This decrease indicates a lower false-positive rate and enhanced conservative prediction reliability. Consequently, based on the optimal delta AICc value, superior OR10 performance, and the principle of model parsimony (Coelho et al., 2019), the parameter set RM = 1 and FC = QHPT was selected as the final optimum.

To validate the effectiveness of parameter optimization, predictive performance was compared between the default (RM = 1, FC = LQHP) and optimized (RM = 1, FC = QHPT) models through ten repeated cross-validation runs. Both models achieved identical average AUC values of 0.947 (Fig. 4), far exceeding the excellent discrimination benchmark of 0.9, confirming their strong capability to explain the environmental response of *B. orientalis* distribution. Notably, while maintaining equally high AUC scores, the optimized model utilized a simpler feature set (QHPT) compared to the default's more complex combination (LQHP), effectively minimizing overfitting risks associated with redundant feature parameters. Combined with the improved OR10 metrics, these findings demonstrate that the optimized parameters not only preserve the predictive accuracy of the original model but also significantly enhance its generalization ability and ecological interpretability.

3.2. Determinants regulating the spatial distribution characteristics of *B. orientalis* in China

Using the optimized MaxEnt model, combined with contribution rate calculation outcomes and Jackknife cross-validation data, this research systematically analyzed the effects exerted by ten habitat variables on the suitable geographical regions where *B. orientalis* could potentially survive. The relative explanatory importance of individual environmental predictors was quantified in descending order of their contribution rates to the habitat suitability model (Fig. 5a). The mean temperature of the driest quarter (Bio9) served as the primary influencing factor, with a contribution rate of 52.6%, followed by annual total precipitation (Bio12) at 34.1%. Other predictors with relatively limited explanatory capacity were ranked as follows: precipitation of the driest quarter (Bio17, 6.8%), isothermality (Bio3, 1.9%), human footprint index in 2000 (HFI, 1.3%), maximum temperature of the warmest month (Bio5, 0.9%), mean temperature of the wettest quarter (Bio8,

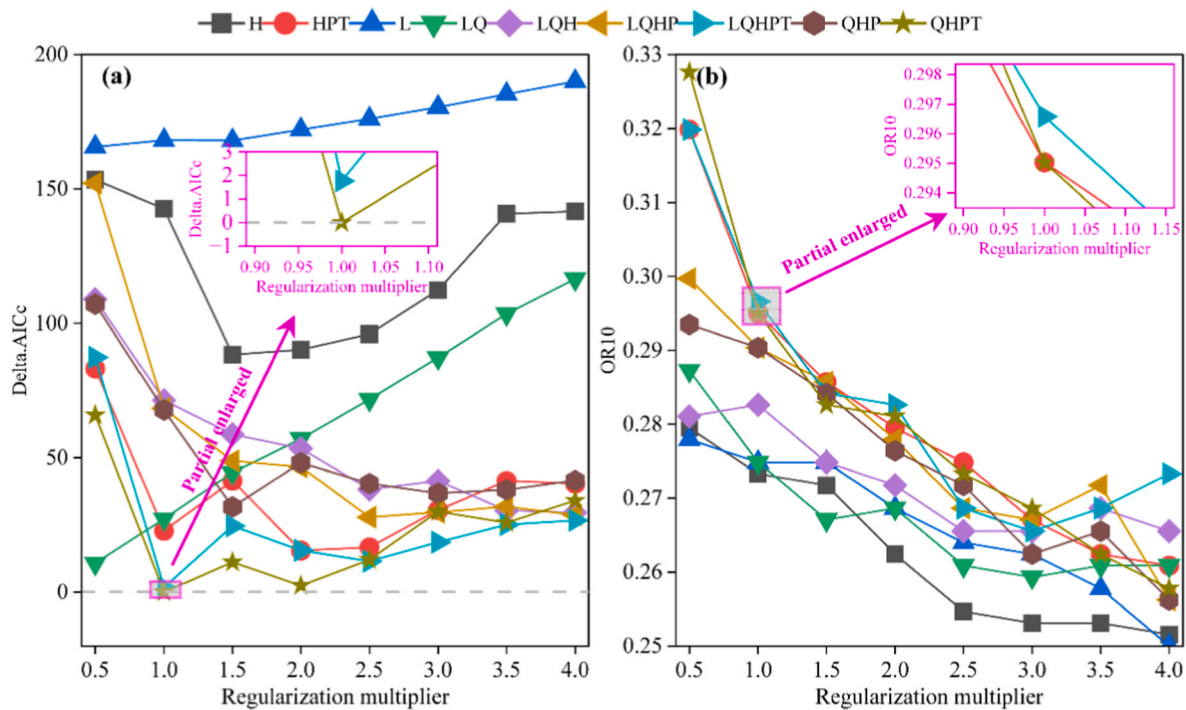


Fig. 3. Delta AICc values from the ENMeval model selection procedure for *B. orientalis*. Feature classes include Linear (L), Quadratic (Q), Hinge (H), Product (P), and Threshold (T). The horizontal grey dashed line indicates the baseline where delta AICc = 0.

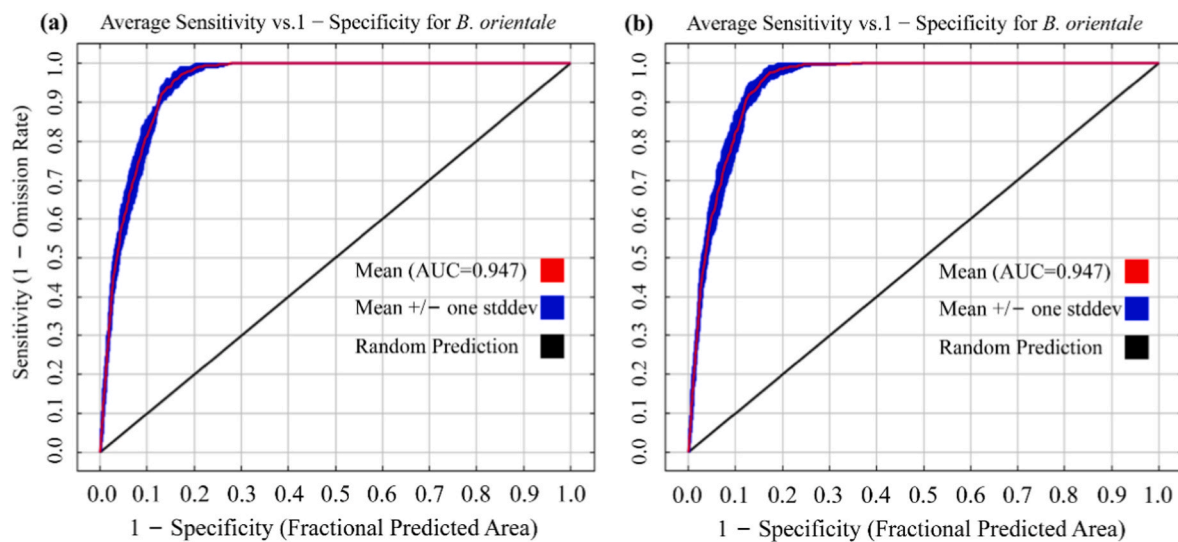


Fig. 4. ROC diagnostic characteristic curves for *B. orientalis* generated via MaxEnt modeling: (a) Area Under the Curve (AUC) using default parameter settings; (b) AUC after parameter tuning.

0.7%), terrain slope (slope, 0.7%), normalized difference vegetation index (NDVI, 0.6%), and terrain aspect (aspect, 0.4%). In terms of variable categories, climatic factors accounted for a cumulative contribution rate of 97.0%. In contrast, anthropogenic, topographic, and vegetation factors contributed merely 1.3%, 1.1%, and 0.6%, respectively, exerting only marginal impacts on the spatial variation of suitable habitats for the target species. Additionally, a jackknife sensitivity test based on regularized training gain was conducted to quantify the independent predictive performance of each individual predictor (Fig. 5b). When the model was run with only one environmental factor

incorporated, Bio12, Bio9, Bio17, NDVI, and Bio8 exhibited the top five standalone predictive capacities. Referring to the mainstream screening criterion that the cumulative contribution rate should exceed 85%, Bio9 and Bio12 jointly explained 86.7% of the spatial heterogeneity in suitable habitat for *B. orientalis*. These two climatic variables overwhelmingly dominate the nationwide spatial distribution pattern of this species, acting as the core climatic determinants that shape its potential geographical distribution across China.

To explore the relationship between the occurrence probability of *B. orientalis* and the two dominant environmental factors, we generated

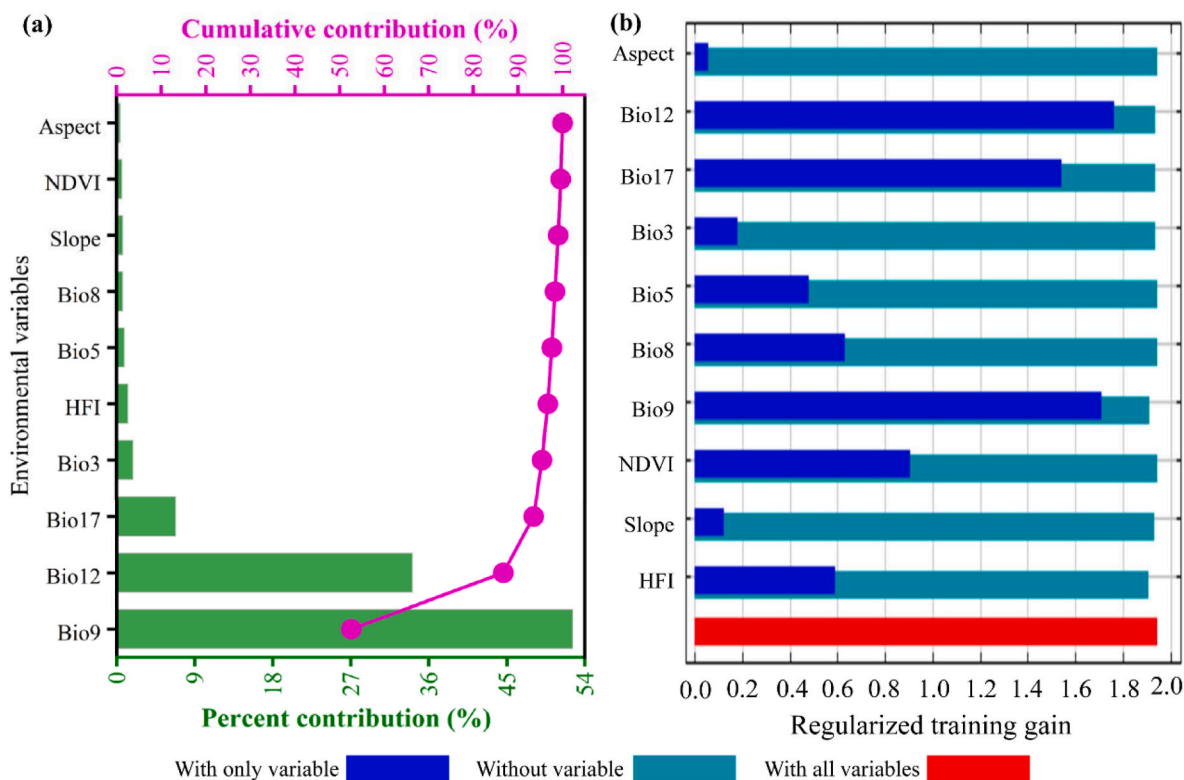


Fig. 5. MaxEnt-based evaluation of environmental variable importance for *B. orientalis*: (a) contribution percentages of individual variables; (b) jackknife analysis of normalized training gain.

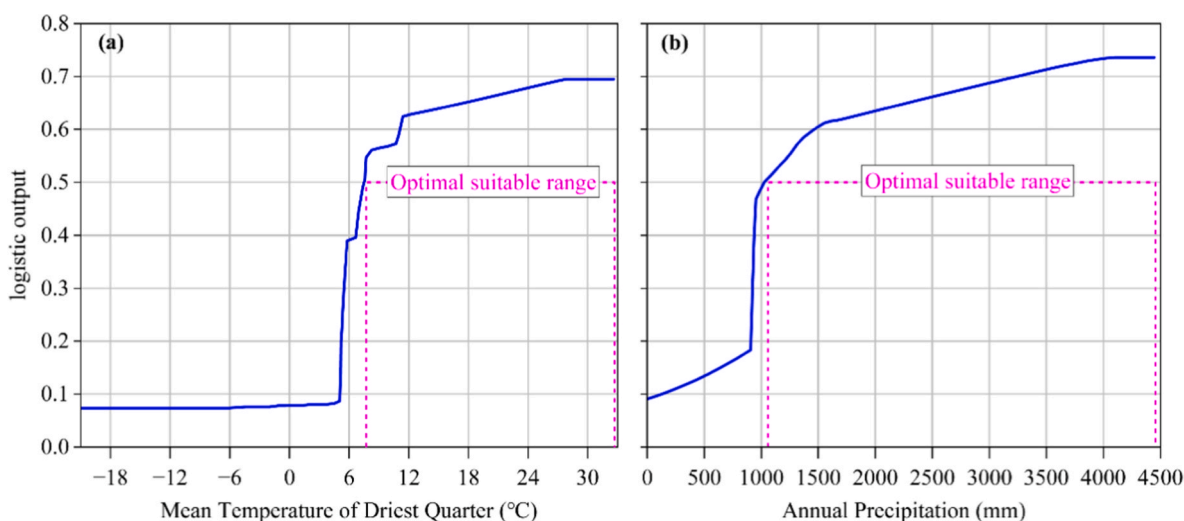


Fig. 6. Predictive response curves for *B. orientalis* habitat suitability based on key bioclimatic variables. Solid blue lines represent the mean predicted probabilities across 10 model iterations, while dashed purple vertical lines indicate the identified optimal environmental thresholds. (a) Mean temperature of driest quarter (Bio9); (b) Annual precipitation (Bio12).

univariate response curves (Fig. 6). For Bio9: within the range of -19.22 to -6.10°C , the occurrence probability remained stable at 0.073 ; it slowly increased to 0.087 between -6.10 and 5.05°C ; then rose sharply to 0.390 within the interval of 5.05 – 5.80°C ; from 5.80 to 8.26°C , the probability rapidly increased to 0.561 ; thereafter, as the temperature rose to 32.60°C , the probability fluctuated between 0.561 and 0.695 , reaching a maximum of 0.695 (Fig. 6a). This indicates that when Bio9 is below -6.10°C , the occurrence probability is extremely low (<0.08), and it remains at a relatively high level once Bio9 exceeds approximately

5.80°C . For Bio12: within the range of 0 – 906.07 mm, the occurrence probability increased from 0.090 to 0.183 ; it rapidly increased to 0.501 between 906.07 and 1027.23 mm; then steadily rose to 0.637 between 1027.23 and 2036.85 mm; beyond 2036.85 mm, the probability slowly increased and stabilized at 0.736 , fluctuating between 0.637 and 0.736 (Fig. 6b). This indicates that suitability is low when precipitation is below 906 mm, and the occurrence probability significantly increases and remains high once precipitation exceeds approximately 1027.23 mm. According to the optimal suitability threshold commonly

used in ecological niche modeling (occurrence probability ≥ 0.5), the most suitable environmental conditions for *B. orientalis* are Bio9 $\geq 5.80^\circ\text{C}$ and Bio12 $\geq 1027.23\text{ mm}$.

3.3. Potential distribution of suitable habitat for *B. orientalis* under current climate

Under current climatic conditions, we predicted the potential suitable habitat of *B. orientalis* in China (Fig. 7). The total area of suitable habitat was approximately $134.24 \times 10^4\text{ km}^2$, accounting for 13.98% of China's total land area. According to the suitability classification, the high-suitability area was approximately $9.00 \times 10^4\text{ km}^2$ (0.94% of China's land area), distributed mainly in patches across most of Taiwan Province, the central and southern parts of Guangdong Province, as well as localized areas of Fujian Province, Hainan Province, Yunnan Province, and Tibet Autonomous Region. The medium-suitability area was approximately $58.79 \times 10^4\text{ km}^2$ (6.12%), distributed continuously across Hainan Province, Guangxi Zhuang Autonomous Region, northern Guangdong Province, Fujian Province, eastern Jiangxi Province, southeastern Hunan Province, southern Zhejiang Province, central Taiwan Province, southwestern Guizhou Province, southern and western Yunnan Province, and southern Tibet. The low-suitability area was approximately $66.45 \times 10^4\text{ km}^2$ (6.92%), distributed mainly across southern Guizhou Province, western Chongqing Municipality, eastern Sichuan Province, western Hunan Province, western Jiangxi Province, southern Anhui Province, eastern Hubei Province, northern Zhejiang Province, and western Hainan Province. These suitability classes are spatially mutually exclusive and together constitute the potential distribution pattern of *B. orientalis* under current climate conditions.

3.4. Spatiotemporal variations in potentially suitable habitats of *B. orientalis* under future climate scenarios

Under the SSP126 climate projection scenario, the overall potential suitable habitat range for *B. orientalis* is projected to reach $166.62 \times 10^4\text{ km}^2$ in the 2050s, which would occupy 17.36% of China's total terrestrial landmass. Specifically, the areas categorized as low, moderate, and high habitat suitability are $62.02 \times 10^4\text{ km}^2$, $85.90 \times 10^4\text{ km}^2$, and $18.70 \times 10^4\text{ km}^2$, respectively. Regions with highly suitable habitats are primarily concentrated in Taiwan Province, southern Guangdong, northeastern Jiangxi, northeastern Guangxi Zhuang Autonomous Region, southern Yunnan, southeastern Xizang, and southern Hainan (Fig. 8a). In the 2070s, the overall extent is projected to experience a mild decline, to $162.81 \times 10^4\text{ km}^2$, equivalent to 16.96% of China's national land area. The corresponding figures for low-, moderate-, and high-suitability categories are $56.62 \times 10^4\text{ km}^2$, $83.62 \times 10^4\text{ km}^2$, and $22.57 \times 10^4\text{ km}^2$, respectively. Meanwhile, the high-suitability zone expands its distribution, covering Taiwan Province, Guangdong Province, Fujian Province, southern Jiangxi, northern Guangxi Zhuang Autonomous Region, southern Yunnan, southeastern Xizang, and southern Hainan (Fig. 8b). Entering the 2090s, the total suitable area rebounds to $174.22 \times 10^4\text{ km}^2$, accounting for 18.15% of China's land territory. The three suitability classes register $54.94 \times 10^4\text{ km}^2$, $89.31 \times 10^4\text{ km}^2$, and $29.97 \times 10^4\text{ km}^2$. The high-suitability habitat continues its outward expansion, with southern Hunan newly incorporated into this core distribution range (Fig. 8c).

Under the SSP245 climate scenario, the overall suitable habitat area was calculated to be $179.64 \times 10^4\text{ km}^2$ in the 2050s, accounting for 18.71% of China's total land area. Specifically, the areas classified as low, moderate, and high suitability reached $64.70 \times 10^4\text{ km}^2$,

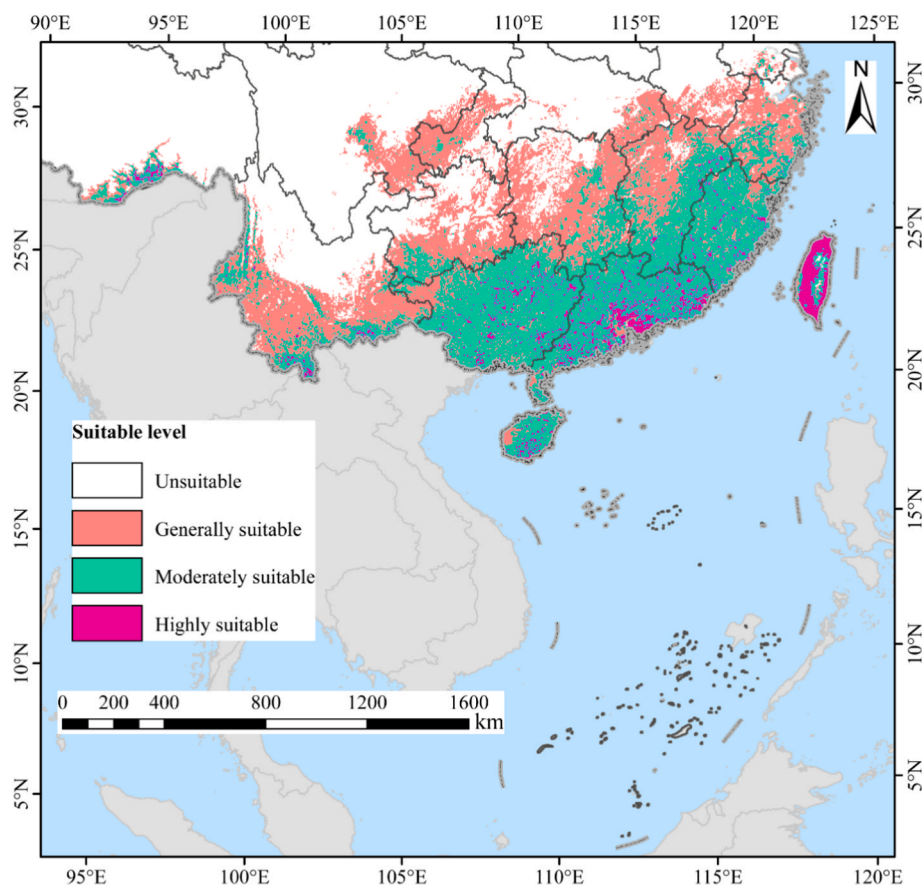


Fig. 7. Present spatial distribution of climate-suitable habitats for *B. orientalis* across China.

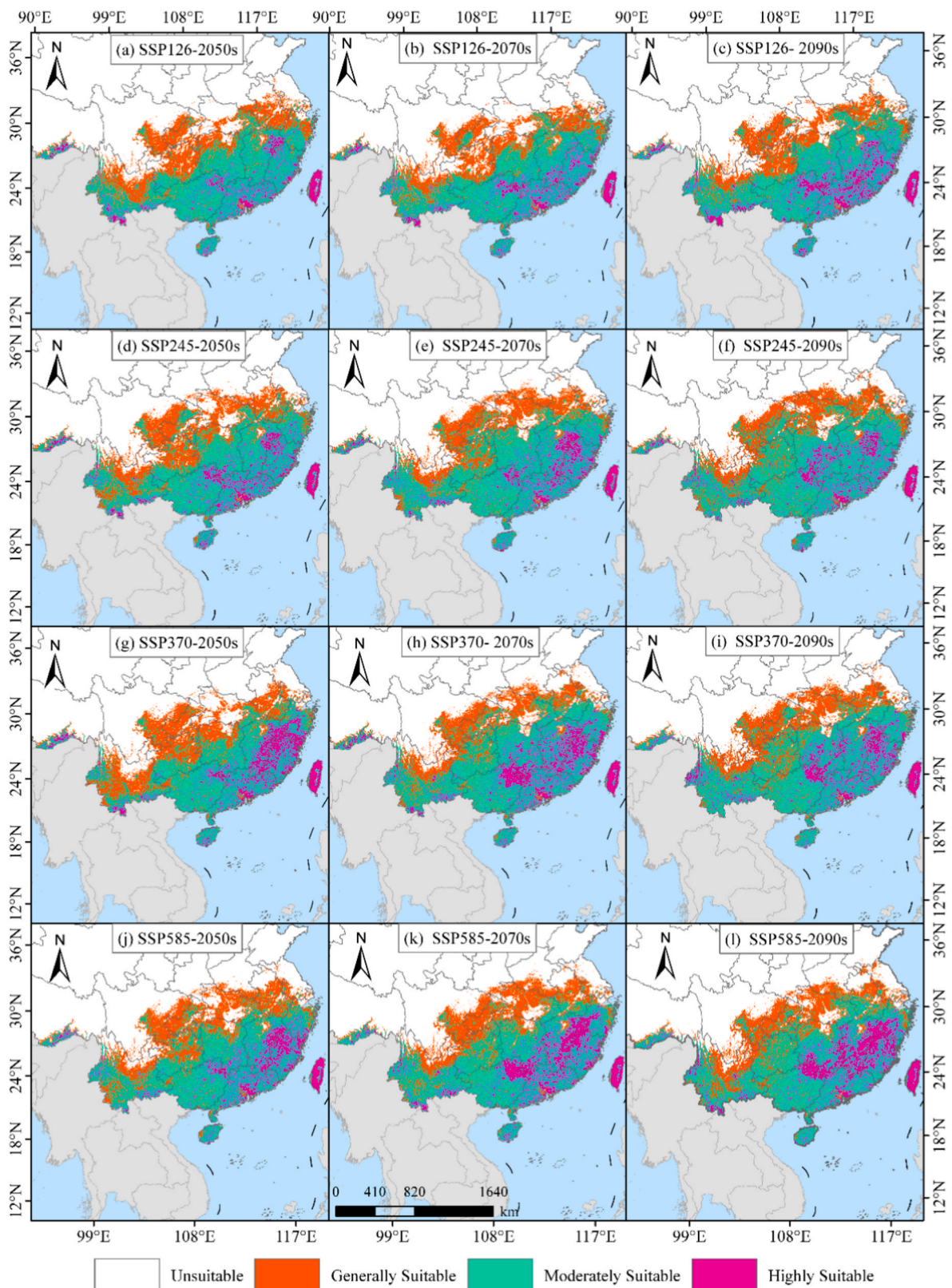


Fig. 8. Predicted climate-suitable distribution areas of *B. orientalis* in China under future climate scenarios.

$90.93 \times 10^4 \text{ km}^2$, and $24.02 \times 10^4 \text{ km}^2$, respectively. Regions with high suitability were primarily concentrated in Taiwan Province, Fujian Province, southern Guangdong Province, the northeastern part of the Guangxi Zhuang Autonomous Region, northeastern Jiangxi Province, southern Yunnan Province, southeastern Xizang Autonomous Region,

and southern Hainan Province (Fig. 8d). Entering the 2070s, the total extent of suitable land rose to $186.85 \times 10^4 \text{ km}^2$, which accounted for 19.46% of the national land area. The corresponding areas of low, moderate, and high suitability were estimated to be $61.63 \times 10^4 \text{ km}^2$, $99.42 \times 10^4 \text{ km}^2$, and $25.80 \times 10^4 \text{ km}^2$. Notably, the scope of highly

suitable zones expanded and covered the majority of Jiangxi Province (Fig. 8e). In the 2090s, the total suitable coverage continued to grow and peaked at $193.19 \times 10^4 \text{ km}^2$ (20.12% of China's land area), with areas of low, moderate, and high suitability being $59.81 \times 10^4 \text{ km}^2$, $108.00 \times 10^4 \text{ km}^2$, and $25.38 \times 10^4 \text{ km}^2$, respectively. Furthermore,

central Hunan Province was newly incorporated into the high-suitability distribution ranges over this period (Fig. 8f).

Under the SSP370 emission scenario, the overall area suitable for the target species reached $170.81 \times 10^4 \text{ km}^2$ in the 2050s, occupying 17.79% of China's land area. This suitable area was divided into three

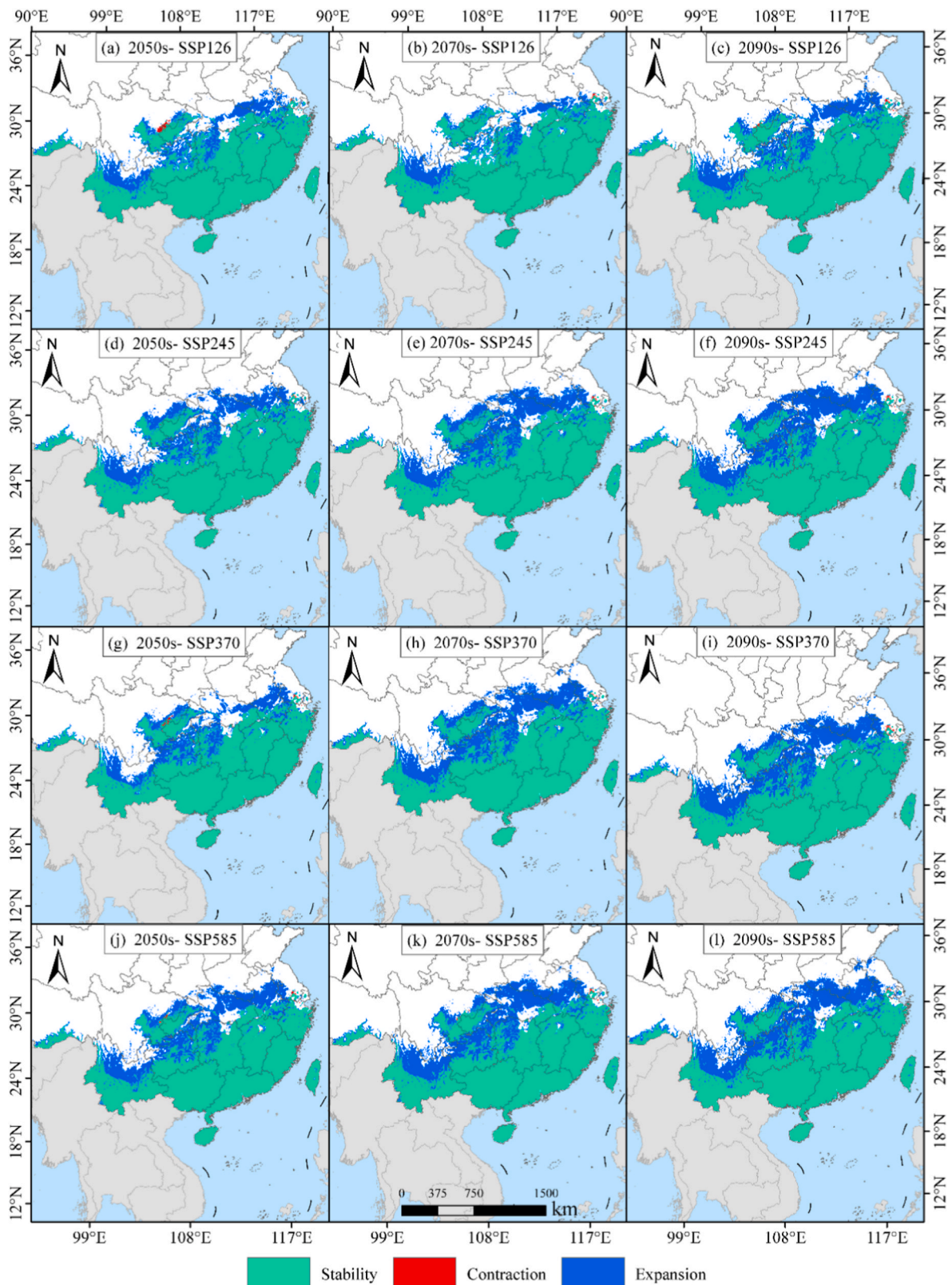


Fig. 9. Future habitat shifts (stability, contraction, expansion) of *B. orientalis* under climate change.

grades: low-suitability areas ($65.44 \times 10^4 \text{ km}^2$), medium-suitability areas ($77.83 \times 10^4 \text{ km}^2$), and high-suitability areas ($27.54 \times 10^4 \text{ km}^2$). High-suitability habitats were geographically occurred in Taiwan Province, Fujian Province, southern Zhejiang Province, eastern Jiangxi Province, southern Hainan Province, southern Guangdong Province, northeastern Guangxi Zhuang Autonomous Region, southern Yunnan Province, and southeastern Xizang Autonomous Region (Fig. 8g). By the 2070s, the overall suitable area had increased substantially to $189.59 \times 10^4 \text{ km}^2$, equivalent to 19.75% of China's land area. The area values for low, medium, and high suitability were updated to $56.00 \times 10^4 \text{ km}^2$, $98.20 \times 10^4 \text{ km}^2$, and $35.39 \times 10^4 \text{ km}^2$, respectively. Moreover, the spatial coverage of high-suitability regions expanded remarkably, encompassing most parts of Guangdong and Jiangxi provinces, as well as central Hunan Province (Fig. 8h). In the 2090s, the total suitable area continued to increase slightly and peaked at $193.35 \times 10^4 \text{ km}^2$ (20.14% of China's land area), with areas of low, medium, and high suitability at $60.49 \times 10^4 \text{ km}^2$, $102.36 \times 10^4 \text{ km}^2$, and $30.50 \times 10^4 \text{ km}^2$, respectively. Furthermore, northwestern Yunnan Province was included in the high-suitability distribution in this period (Fig. 8i).

Under the SSP585 climate scenario, the projected suitable habitat for the 2050s was estimated at $182.07 \times 10^4 \text{ km}^2$, representing 18.97% of China's terrestrial territory. Breaking this down, the three suitability classes (low, moderate, and high) accounted for $66.34 \times 10^4 \text{ km}^2$, $89.72 \times 10^4 \text{ km}^2$, and $26.00 \times 10^4 \text{ km}^2$, in that order. Highly suitable patches were chiefly scattered across Taiwan Province, Fujian Province, Guangdong Province, the eastern part of Jiangxi Province, southern Zhejiang Province, the northeastern section of Guangxi Zhuang Autonomous Region, southern Yunnan Province, southern Hunan Province, the southeastern corner of Xizang Autonomous Region, and southern Hainan Province (Fig. 8j). Moving to the 2070s, the total suitable extent enlarged to $191.47 \times 10^4 \text{ km}^2$, covering 19.94% of the national territory. The three suitability tiers corresponded to low- ($63.40 \times 10^4 \text{ km}^2$), moderate- ($92.50 \times 10^4 \text{ km}^2$), and high-suitability ($37.41 \times 10^4 \text{ km}^2$) zones. High-suitability areas witnessed conspicuous gains, expanding into most parts of Jiangxi Province (Fig. 8k). By the 2090s, the overall suitable area climbed further to $194.20 \times 10^4 \text{ km}^2$, equivalent to 20.23% of China's land surface. The three suitability tiers corresponded to $62.90 \times 10^4 \text{ km}^2$ (low), $93.89 \times 10^4 \text{ km}^2$ (medium), and $37.41 \times 10^4 \text{ km}^2$ (high). During this final period, high-suitability habitats were heavily concentrated in Taiwan Province, Fujian Province, southern Zhejiang Province, Jiangxi Province, southern Guangdong Province, the northeastern part of Guangxi Zhuang Autonomous Region, southern Hunan Province, southern Yunnan Province, and southeastern Xizang Autonomous Region (Fig. 8l).

3.5. Temporal dynamics of suitable habitat extent for *B. orientalis* under future climate projections

Fig. 9 presents the spatial distribution of persistent, lost, and newly gained suitable habitats for *B. orientalis* under future climate scenarios, while Table 1 summarizes the corresponding areas and percentages. Under the SSP126 pathway (Fig. 9a–c), the total suitable habitat for this species showed no substantial change relative to its current extent. In the 2050s, the stable habitat covered $134.18 \times 10^4 \text{ km}^2$, compared with $0.83 \times 10^4 \text{ km}^2$ of contraction and $32.77 \times 10^4 \text{ km}^2$ of expansion, translating to stability and expansion rates of 79.98% and 19.53%, respectively. By the 2070s, the stable area rose slightly to $134.60 \times 10^4 \text{ km}^2$, whereas both contraction ($0.41 \times 10^4 \text{ km}^2$) and expansion ($28.62 \times 10^4 \text{ km}^2$) areas diminished, yielding rates of 82.26% and 17.49%. In the 2090s, the stable area remained almost constant at $134.61 \times 10^4 \text{ km}^2$, yet the expansion area rebounded to $39.97 \times 10^4 \text{ km}^2$, resulting in rates of 76.93% and 22.84%, respectively.

For the SSP245 trajectory (Fig. 9d–f), a continuous expansion of suitable habitat for *B. orientalis* was observed in comparison with the present-day baseline. In the 2050s, the persistent area was recorded at $134.77 \times 10^4 \text{ km}^2$, accompanied by $0.24 \times 10^4 \text{ km}^2$ of contraction and $45.53 \times 10^4 \text{ km}^2$ of expansion, which translated into stability and expansion proportions of 74.65% and 25.22%. By the 2070s, the stable area was estimated at roughly $134.78 \times 10^4 \text{ km}^2$, while the expanded area climbed to $52.46 \times 10^4 \text{ km}^2$, yielding adjusted rates of 71.89% and 27.98%. In the 2090s, the expansion area rose further to $58.62 \times 10^4 \text{ km}^2$, with the stability proportion dropping to 69.59% and the expansion proportion increasing to 30.28%.

For the SSP370 trajectory (Fig. 9g–i), *B. orientalis* also shows an expansion trend in its suitable habitat relative to the current distribution. In the 2050s, the persistent habitat covers $134.52 \times 10^4 \text{ km}^2$, with contraction and expansion areas of $0.49 \times 10^4 \text{ km}^2$ and $36.62 \times 10^4 \text{ km}^2$, respectively, corresponding to stability and expansion rates of 78.38% and 21.34%. Subsequently, by the 2070s, the expansion area surges to $54.87 \times 10^4 \text{ km}^2$, shifting the rates to 71.02% and 28.90%. In the 2090s, the newly gained habitat climbs further to $59.02 \times 10^4 \text{ km}^2$, yielding rates of 69.44% and 30.42%.

Under the SSP585 pathway (Fig. 9j–l), the most substantial expansion of suitable habitat for *B. orientalis* was observed relative to the present-day baseline. In the 2050s, the persistent habitat was recorded at $134.62 \times 10^4 \text{ km}^2$, accompanied by $0.38 \times 10^4 \text{ km}^2$ of contraction and $47.85 \times 10^4 \text{ km}^2$ of expansion, which translates into stability and expansion proportions of 73.62% and 26.17%. Thereafter, by the 2070s, the gain area rose dramatically to $57.19 \times 10^4 \text{ km}^2$, yielding adjusted rates of 70.10% and 29.76%. In the 2090s, the expanded habitat further ascended to $59.64 \times 10^4 \text{ km}^2$, with the stability share dropping to 69.25% and the expansion share rising to 30.64%.

Table 1

Dynamics in habitat suitability area for *B. orientalis* under projected climatic conditions. Stability, contraction, and expansion rates were calculated using the sum of stable, contracted, and expanded areas as the denominator (100%). Note that these three rates sum to 100% within each scenario-period combination.

Period	Area (10^4 km^2)			Rate of change (%)		
	Stability	Contraction	Expansion	Stability	Contraction	Expansion
SSP126-2050s	134.18	0.83	32.77	79.98	0.49	19.53
SSP126-2070s	134.60	0.41	28.62	82.26	0.25	17.49
SSP126-2090s	134.61	0.40	39.97	76.93	0.23	22.84
SSP245-2050s	134.77	0.24	45.53	74.65	0.13	25.22
SSP245-2070s	134.78	0.23	52.46	71.89	0.12	27.98
SSP245-2090s	134.74	0.26	58.62	69.59	0.13	30.28
SSP370-2050s	134.52	0.49	36.62	78.38	0.28	21.34
SSP370-2070s	134.84	0.15	54.87	71.02	0.08	28.90
SSP370-2090s	134.72	0.28	59.02	69.44	0.14	30.42
SSP585-2050s	134.62	0.38	47.85	73.62	0.21	26.17
SSP585-2070s	134.72	0.28	57.19	70.10	0.15	29.76
SSP585-2090s	134.80	0.20	59.64	69.25	0.10	30.64

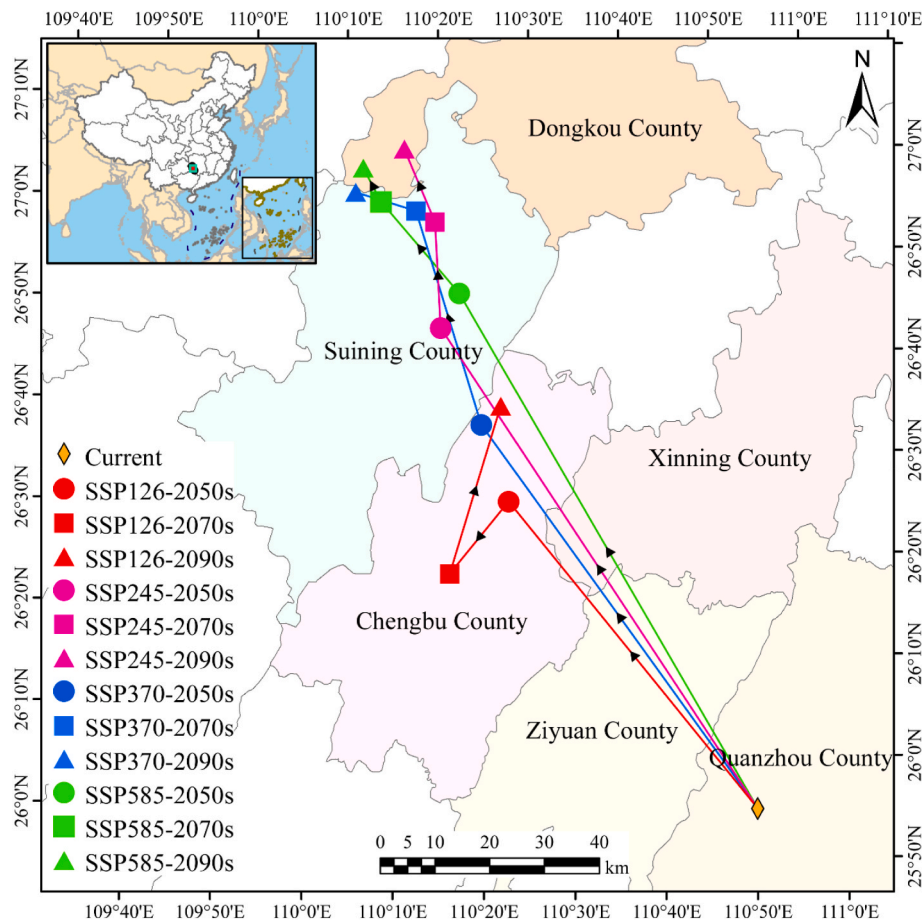


Fig. 10. Temporal and spatial dynamics of habitat centroid for *B. orientalis* under multiple climate scenarios.

3.6. Spatial migration of core suitable habitat centroids for *B. orientalis* under projected future climate backgrounds

The geographical center of the current natural distribution range of *B. orientalis* is located in Shaoshui Town, Quanzhou County, Guilin City, Guangxi Zhuang Autonomous Region (110°51'E, 25°56'N). Overall, the distribution centroid exhibits a consistent northwestward trend across all future climate scenarios, with the sole exception of a brief southwesterly deviation under SSP126 (Fig. 10). For the SSP126 scenario, the centroid moves ~72.27 km northwest to Maoping Town, Chengbu County, Hunan Province (110°25'E, 26°27'N) in the 2050s. It then shifts ~17.06 km southwest to Rulin Town, Chengbu County (110°18'E, 26°20'N) in the 2070s, and finally migrates ~31.99 km northeast to Xiyan Town, Chengbu County (110°25'E, 26°37'N) in the 2090s. In terms of the SSP245 scenario, the centroid migrates ~105.19 km northwest to Wuyang Town, Suining County, Hunan Province (110°19'E, 26°45'N) by the 2050s, then shifts ~19.40 km northward to Wawutang Town, Suining County (110°19'E, 26°55'N) by the 2070s, and subsequently moves ~14.42 km further northwest to Luoxi Township, Dongkou County, Hunan Province (110°16'E, 27°02'N) in the 2090s. Under the SSP370 scenario, the centroid undergoes an ~86.45 km northwest shift to Tuanshan Town, Shaodong County, Hunan Province (110°22'E, 26°35'N) in the 2050s, continues ~40.79 km northwest to Shuikou Township, Suining County (110°17'E, 26°56'N) by the 2070s, and finally displaces ~11.58 km northwest to Matang Township, Suining County (110°10'E, 26°58'N) in the 2090s. As for the SSP585 scenario, the centroid moves ~108.75 km northwest to Tangjiafang Town, Suining County, Hunan Province (110°21'E, 26°48'N) by the 2050s, then shifts another ~21.99 km northwest to Matang Township, Suining County (110°13'E, 26°57'N) by the 2070s, and ultimately migrates

~6.96 km northwest to Weijiaqiao Town, Dongkou County, Hunan Province (110°11'E, 27°01'N) in the 2090s.

4. Discussion

4.1. Model optimization and its implications for distribution modeling of *B. orientalis*

According to the findings of this research, the original parameter combination RM = 1 and FC = LQHP delivered a delta AICc value of 68.32, well above the underfitting cutoff of 2 documented in [Anderson and Gonzalez \(2011\)](#). In contrast, the refined parameter scheme (RM = 1 and FC = QHPT) returned a delta AICc equal to 0, cut the OR10 metric by 0.53%, and retained an AUC value of 0.947. Although the 646 occurrence records used in this study do not constitute a small sample in the strict sense ($n < 30$), optimization still significantly reduced the false positive rate (OR10 decreased from 0.2966 to 0.2950). This finding is consistent with the review by [Morales et al. \(2017\)](#), which noted that more than 60% of MaxEnt studies still use default parameters, and that the risk of overfitting under small-sample conditions is systematically underestimated. [Kass et al. \(2021\)](#) emphasized that the configuration with delta AICc < 2 and the most parsimonious feature combination should be adopted as the standard, and [Valavi et al. \(2022\)](#) confirmed that parameter-optimized models improve performance on independent validation sets by an average of 12–15%. The necessity of parameter optimization is further underscored by studies on ferns. [Wang et al. \(2016\)](#) reported that unoptimized models inflated habitat fragmentation estimates by approximately 30%, and [Wei et al. \(2021\)](#) demonstrated that default feature combinations introduce systematic bias in predicted probabilities. Ferns exhibit both long-distance spore dispersal

capacity and pronounced environmental sensitivity during the gametophyte stage (Blake-Mahmud et al., 2025), with their environmental response nonlinearity substantially exceeding that of seed plants. Overly complex feature combinations thus risk misinterpreting spatial noise as ecological signals. Accordingly, we recommend that parameter optimization be adopted as a standard procedure in future distribution modeling studies on ferns.

4.2. Dominant effects of temperature and precipitation on the spatial distribution of *B. orientalis*

The present work verified Bio9 and Bio12 as the primary environmental variables governing the geographic distribution of *B. orientalis*, which together accounted for a total contribution of 86.7%. According to the global-scale study by Qian et al. (2023), spatial heterogeneity in fern phylogenetic structure is largely governed by temperature and precipitation, with these two climatic factors collectively explaining 26% to 36% of the total variation. Michael and Jürgen (2022) studied Andean ferns and similarly found that water availability during the driest quarter is a key threshold limiting fern elevational distribution. However, in this study, the contribution rate of Bio9 (52.6%) far exceeded those of extreme maximum temperature (0.9%) and isothermality (1.9%). This pattern may reflect two non-exclusive mechanisms. First, the strong sensitivity of ferns to moisture and temperature stress during the driest quarter reflects a fundamental ecological requirement shared by most fern species, particularly at the gametophyte stage, which alone could explain much of the Bio9 signal.

Second, the REE hyperaccumulation function may impose an additional constraint. As found by He et al. (2025), rare earth elements in *B. orientalis* exist as nanoscale monazite within leaf cells, and their formation depends on transpiration-driven REE uptake and phosphate precipitation. Low temperatures and drought during the driest quarter inhibit stomatal conductance and transpiration rates (Brodrick and McAdam, 2011), thereby disrupting the chain of REE uptake, transport, and precipitation. This mechanism also explains why the driest quarter, rather than the warmest quarter, may act as a limiting factor: REE uptake relies on sustained water flow, not merely on transpiration peaks under high temperatures. Corzo-Remigio et al. (2026) screened fern specimens from Australia and Pacific islands and found that newly discovered REE hyperaccumulator ferns are mainly distributed in tropical and subtropical humid climate zones. The response curves in this study established quantitative thresholds: an occurrence probability ≥ 0.5 requires Bio9 $\geq 5.80^\circ\text{C}$ and Bio12 $\geq 1027.23\text{ mm}$, thresholds that highly overlap with the climatic conditions of the ion-adsorption REE ore districts in South China. However, the relative weight of the REE-related constraint versus the fundamental ecological requirements of ferns cannot be quantified with the current occurrence-based modeling approach. The REE-related mechanism should therefore be regarded as a plausible complementary explanation rather than the primary driver of the observed pattern. Disentangling these effects will require crossed temperature-control and REE-addition experiments, as well as comparative modeling of co-occurring non-hyperaccumulating ferns under identical climate scenarios.

4.3. Current distribution patterns and their coincidence with geological REE backgrounds

Although the current climate could support a total potential habitat of $134.24 \times 10^4\text{ km}^2$ for *B. orientalis*, the high-suitability fraction remains disproportionately small (0.94%). This limited high-quality habitat is not contiguous but instead occurs as discrete patches, predominantly located in Taiwan Province, the central and southern regions of Guangdong Province, and Hainan Province. Michael and Jürgen (2022) studied global mountain ferns and showed that the gametophyte stage of ferns is highly sensitive to water and temperature stress, which limits fern colonization in arid or extreme environments. Consequently,

although many fern species are widespread at regional scales, their high-quality suitable habitats are often confined to specific moist microhabitats. Notably, there is significant spatial overlap between the high-suitability areas and the distribution of ion-adsorption REE ore deposits in South China: most of the Taiwan Province, central and southern Guangdong Province, southern Fujian Province, Hainan Province, and southwestern Yunnan Province exactly cover the main distribution range of the southern Jiangxi–northern Guangdong–western Fujian ion-adsorption REE ore belt. Purwadi et al. (2025) studied Bangka Island, Indonesia, and demonstrated that soil exchangeable REE content is a key local factor controlling the degree of REE hyperaccumulation in ferns. A review by Liu et al. (2025a) found that 9 out of 12 reported REE hyperaccumulator plant species in China are distributed within or adjacent to ion-adsorption REE ore districts. Huang et al. (2026) pointed out that the unique REE occurrence form developed through weathering and leaching in South China provides a geochemical prerequisite for REE uptake by hyperaccumulator plants. Therefore, the high-suitability areas may represent regions with both climatic suitability and high geological background. Furthermore, the contribution rate of the Human Footprint Index to suitable habitat distribution was only 1.3%, consistent with the global analysis by Venter et al. (2016), indicating that human activity is not a dominant factor at the macroscale. However, attention should still be paid to habitat fragmentation in locally high-HFI areas, with the Pearl River Delta urban agglomeration corridor and the southern edge of the Yangtze River Delta serving as notable examples. This aligns with the findings of Gao et al. (2022) and Wan et al. (2026) that human activities have led to population fragmentation of plants in evergreen broad-leaved forests.

4.4. Future climate change driven net range expansion and northwestward centroid shift of *B. orientalis*

Unlike the range contractions projected for many rare and endangered plants, *B. orientalis* exhibits net expansion under all CMIP6 scenarios, with a maximum contraction area of only $0.83 \times 10^4\text{ km}^2$, a maximum expansion area of $59.64 \times 10^4\text{ km}^2$, and stability rates of 69%–82%. Ferns are generally considered to have high long-distance dispersal potential due to their efficient spore dispersal mechanisms (Qian et al., 2026), which may partly explain the strong adaptability of *B. orientalis* to future climate change. However, the projected expansion magnitude (high-suitability area increasing from $9.00 \times 10^4\text{ km}^2$ to $37.41 \times 10^4\text{ km}^2$) far exceeds general expectations, suggesting that beyond dispersal ability, physiological plasticity may also play an important role. Previous studies have shown that appropriate concentrations of rare earth elements can significantly boost the function of antioxidant enzymes (e.g., peroxidase and catalase) in plants (Peng et al., 2013), thereby enhancing plant tolerance to oxidative stress. As a speculative mechanism, the high REE concentration in *B. orientalis*, a known REE hyperaccumulator, may indirectly enhance its physiological tolerance to climatic stresses such as high temperature by strengthening the antioxidant defense system, thereby partially explaining its exceptionally pronounced range expansion as climate conditions shift in the future. Nonetheless, this causal chain has not yet been directly experimentally verified in *B. orientalis*, and future studies should test it using crossed experiments of temperature control and REE addition.

However, net expansion does not imply the absence of risk. Propagule dispersal limitation is a key factor limiting plant population establishment (Hooftman et al., 2021; Levin, 2021). A meta-analysis by Hargreaves et al. (2014) of 111 transplant experiments beyond range boundaries showed that species performance outside their range boundaries declined by an average of approximately 40%–45%, with 83% of tests using lifetime fitness as an indicator showing significant declines. Among studies on geographic range boundaries, up to 83% of cases showed that the actual distribution range of species is smaller than their potential viable range, primarily attributable to dispersal limitation. Therefore, even if climate projections indicate range expansion, the

future expansion potential of *B. orientalis* may still be constrained by dispersal bottlenecks. Regarding centroid migration, the centroid of suitable habitat for *B. orientalis* generally shifts northwestward, migrating 108.75 km by SSP585-2090s to southwestern Hunan Province. This trend is directionally consistent with the global meta-analysis by [Lenoir et al. \(2020\)](#) on climate change-induced species distribution shifts toward poles and higher elevations, i.e., species distributions generally shift toward colder regions. Notably, under SSP126, the centroid exhibits fluctuations, whereas under high-emission scenarios, it consistently advances northwestward, suggesting that under low-emission scenarios, internal climate variability dominates the fluctuations, while under high-emission scenarios, the long-term trend signal outweighs the noise. From an application perspective, the northwestward migration of the centroid toward southwestern Hunan implies that the current REE phytomining pilot sites in Guangdong and Guangxi may need to be strategically relocated northward by the end of this century to match the spatial migration trend of the suitable habitat of *B. orientalis*.

It should be noted that the centroid migration reported here represents the geometric displacement of climatically suitable habitat, not the actual migration of *B. orientalis* populations. Whether the species can track this shifting climate envelope depends on its dispersal capacity. Although fern spores can disperse tens to hundreds of kilometers under favorable winds, most are deposited within a few kilometers of the source. The projected maximum displacement (108.75 km by SSP585-2090s, ~1.4 km/year) falls within the upper range of plausible long-distance dispersal, but successful colonization also requires suitable microhabitats and, for this REE hyperaccumulator, adequate soil REE availability. The effective migration rate may therefore be substantially lower than the geometric centroid shift. Conservation planning should thus consider both habitat shifts and dispersal constraints, and evaluate assisted migration or ex situ conservation where natural dispersal cannot keep pace with climate change.

4.5. Spatial guidance for REE phytomining and conservation planning of *B. orientalis*

The findings of this research establish a definite spatial reference system for the on-site protection of *B. orientalis* and its application in rare earth element (REE) phytomining. For in-situ conservation planning, conservation priority zones ought to be designated in stable habitats that are currently suitable for the survival of this species. Specifically, these priority areas refer to habitats that can still maintain high suitability amid ongoing future climate changes, with the junction of Guangxi Zhuang Autonomous Region, Guangdong Province and Fujian Province serving as the core key region. Geographically, this junction area lies close to the modern distribution center of *B. orientalis* (Quanzhou County in Guangxi Zhuang Autonomous Region), and also acts as the initial migration zone where the species' overall distribution center shifts toward the northwest. [van der Ent et al. \(2026\)](#) emphasized that protecting natural hyperaccumulator populations is a prerequisite for ensuring sustainable utilization of this species.

Regarding REE phytomining, priority pilot areas should be established in newly added high-suitability areas within the expansion zones under projected future environments. For example, by the 2090s under the SSP245 trajectory, eastern Jiangxi Province and southern Hunan Province are predicted to become high-suitability areas, with the high-suitability coverage in Jiangxi Province significantly expanding and central Hunan Province newly added as a high-suitability area. Considering the relatively distant time scale (2070–2090), we recommend prioritizing small-scale preliminary trials in the expansion areas of SSP126-2050s, such as western Fujian Province, southern Jiangxi Province, and northern Guangdong Province, to verify the actual REE accumulation efficiency of *B. orientalis* in these newly suitable areas. [Huang et al. \(2026\)](#) pointed out that conducting field trials to verify the operational feasibility of phytomining at a commercial scale is crucial,

and the expansion areas identified in this study provide clear spatial guidance for such trials.

However, climatic suitability does not necessarily equate to phytomining suitability. Although current high-suitability habitats largely coincide with the ion-adsorption REE ore belts in South China, many of these projected expansion areas lie outside or only marginally overlap with known REE-enriched soils. There, insufficient soil REE background could limit REE accumulation even under favorable climate. We therefore recommend soil geochemical screening before field trials, and prioritizing sites where climatic suitability and REE-enriched soils coincide. Where overlap is limited, expansion areas may serve conservation and germplasm preservation rather than commercial phytomining. The extent to which these recommendations apply across China's ion-adsorption REE mining areas remains uncertain. Phytomining yield is determined jointly by biomass production and foliar REE concentration, and the biomass of *B. orientalis* is lower than that of *Dicranopteris* species. *B. orientalis* may therefore be most suitable where the recovery of monazite-bound REE is prioritized, whereas *Dicranopteris* may be preferable, or complementary, where biomass yield is the main objective or where site conditions lie outside the climatic optimum of *B. orientalis*. Field trials across contrasting soil and climatic conditions are required before either species is deployed at scale.

Regarding ex situ conservation and germplasm resource protection, the centroid migration pathway (Quanzhou County, Guangxi Zhuang Autonomous Region → Chengbu County, Hunan Province → Suining County, Hunan Province → Dongkou County, Hunan Province) provides a spatial guideline for the layout of off-site preservation and germplasm resource banks. In summary, we recommend establishing mining exclusion zones within stable areas to protect core populations, setting up rotational phytomining trial fields within expansion areas where soil REE background is confirmed, and arranging germplasm resource banks and artificial breeding bases along the centroid migration axis to address both conservation and utilization needs in response to climate scenarios.

4.6. Limitation and future work

This study has several limitations. First, spatially explicit, high-resolution soil REE data across China remain scarce and fragmented, with no unified public database currently available. We therefore could not generate the requested map overlaying current REE-enriched soils with the geographical distribution of *B. orientalis* and its projected shifts under climate change. This data gap also means that climatic suitability cannot be equated with phytomining suitability: many projected expansion areas may lie outside known REE-enriched soils, where insufficient soil REE background could limit accumulation even under favorable climate. Second, propagule dispersal limitation was not incorporated, so projected expansion areas may not be fully colonized. Third, soil physicochemical properties (e.g., pH, exchangeable REE concentrations) were not included as predictors. Fourth, only a single GCM (BCC-CSM2-MR) was used, leaving inter-model uncertainty unquantified.

Future work should address these four limitations correspondingly: (1) compiling regional soil geochemical survey data and conducting portable X-ray fluorescence measurements, combined with machine-learning-based digital soil mapping, to generate high-resolution REE availability layers that can be directly overlaid with MaxEnt projections; (2) incorporating propagule dispersal models and transplant experiments to assess the colonization potential of projected expansion areas (3) adding soil physicochemical variables (e.g., pH, organic matter, exchangeable REE); to build coupled climate–soil suitability models; and (4) applying multi-GCM ensembles to reduce inter-model uncertainty.

5. Conclusions

Using an optimized MaxEnt model, we quantified for the first time

the climatic influences on the distribution of *B. orientalis*, a REE-hyperaccumulating fern in China. Temperature (Bio9) and moisture (Bio12) emerged as the overriding factors, collectively contributing 86.7% to the model prediction. The present work also found that this species exhibits net expansion under all CMIP6 scenarios (maximum expansion area reaching $59.64 \times 10^4 \text{ km}^2$, while the maximum contraction area was only $0.83 \times 10^4 \text{ km}^2$), with the centroid of suitable habitat shifting northwestward by up to approximately 108.75 km. The dominance of Bio9 likely reflects the general moisture and temperature requirements of ferns during the driest quarter, with the transpiration dependence of REE uptake possibly imposing an additional constraint on the climatic niche of this hyperaccumulator. Methodologically, the optimized model (RM = 1, FC = QHPT) reduced the false positive rate by 0.53% compared to default parameters, establishing a reproducible optimization paradigm for fern distribution modeling. Based on these findings, we recommend targeting the Guangxi Zhuang Autonomous Region–Guangdong Province–Fujian Province border region as a priority in situ conservation area, deploying REE phytomining pre-trials in areas including northern Guangdong, western Fujian, and southern Jiangxi, as well as arranging germplasm resource banks along the Quanzhou City (Fujian Province)–Chengbu Miao Autonomous County (Hunan Province)–Suining County (Hunan Province)–Dongkou County (Hunan Province) axis. This study did not account for propagule dispersal limitation or spatial heterogeneity in soil available REE content, and the causal relationship between expansion mechanisms and REE hyperaccumulation remains to be validated through crossed experiments of temperature control and REE addition.

CRedit authorship contribution statement

Jun Ren: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Suhang Li:** Visualization, Software, Formal analysis. **Longcheng Jiang:** Visualization, Formal analysis, Data curation. **Qiong Yang:** Software, Data curation. **Yudan Cai:** Visualization, Data curation. **Liyuru Chen:** Visualization, Data curation. **Yangzhou Xiang:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition. **Bin Yao:** Writing – review & editing, Writing – original draft, Project administration. **Yuan Li:** Writing – review & editing, Writing – original draft, Project administration.

Informed consent statement

Not applicable.

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Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.indic.2026.101562>.

Data availability

Data will be made available on request.

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