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Optimizing MaxEnt to project habitat shifts of *Idesia polycarpa* var. *vestita* Diels, a bioenergy tree, in China under climate change scenarios

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ABSTRACT

Climate change is reshaping the distribution of plant species worldwide, yet the ecological niche and future habitat trajectories of *Idesia polycarpa* var. *vestita* Diels (*I. vestita*), a dioecious bioenergy tree native to subtropical China, remain unknown. We compiled 241 quality-controlled georeferenced occurrence records and selected ten statistically independent environmental predictors for modeling. We optimized the MaxEnt model feature combination and regularization multiplier (FC = LQ, RM = 0.5) using ENMeval with AICc minimization, and the final model exhibited excellent predictive performance (AUC = 0.945, TSS = 0.831). Minimum temperature of the coldest month (Bio6, 33.4%) and annual precipitation (Bio12, 33.2%) jointly dominated the species' distribution. The optimal niche comprises mild winters (Bio6: −4.79°C to 1.46°C), abundant precipitation (>600 mm), moderate temperature seasonality (Bio4: 604–884), and mid-to low-elevation mountains (369–2647 m). Under SSP126, total suitable habitat remains stable, whereas under SSP245, SSP370 and SSP585, progressive habitat contraction occurs, with highly suitable areas nearly disappearing by the 2090s under the highest-emission SSP585 scenario. Notably, SSP245 shows a transient expansion followed by delayed contraction, a pattern consistent with the adaptive lag hypothesis in this long-lived tree, though direct demographic validation is currently lacking. Habitat loss concentrates in southern low-elevation margins, whereas gains emerge in the Qinba Mountains and the southeastern Qinghai–Tibet Plateau. The distribution centroid shifts northwestward from Hunan Province toward the Wuling–Wushan mountain system, with displacement increasing with radiative forcing. These findings identify the Qinba and Wuling Mountains as long-term refugia. We therefore recommend prioritizing these areas for in situ germplasm conservation while gradually relocating plantations from climatically vulnerable southern margins toward future high-suitability zones in western Hubei and eastern Chongqing. This optimized MaxEnt framework provides a science-based foundation for industrial planning and climate-adaptive conservation of *I. vestita* under global change.

1. Introduction

Global climate change driven by human activities has become a primary force reshaping the biogeographic patterns of biodiversity. Rising temperatures are forcing species to shift their ranges toward higher latitudes and elevations, and this biological redistribution is already affecting ecosystem functions and human well-being [1,2]. For plants, climate warming manifests in multiple ways: disrupted

phenological rhythms [3,4], reorganized community structure [5], and shifting geographic distributions [6,7]. These distributional changes largely reflect the tendency of species to track their fundamental climatic niches [8]. Woody perennials, in particular, are inherently slow to respond to rapid climate change due to their long generation times, delayed reproductive maturity, and limited seed dispersal [9,10]. When actual distributions become decoupled from suitable climatic space, local extinctions and range contractions become likely, posing serious

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threats to forest ecosystem integrity and the sustainability of commercial forestry [11,12]. Therefore, accurately predicting how economically valuable native tree species might shift their suitable habitats under future climate scenarios is critical for guiding plantation zoning, germplasm conservation, and long-term industry planning [13,14].

Among the available tools, ecological niche models, particularly the MaxEnt model based on maximum entropy, have become widely used for converting complex, nonlinear relationships between species occurrence and environmental factors into explicit potential distribution maps. MaxEnt requires only presence data and performs well even with small sample sizes [15–17]. This model has been successfully applied to predict climate-driven distribution shifts across various taxa [18,19]. However, a growing body of methodological work emphasizes that the reliability of MaxEnt predictions depends heavily on systematic parameter optimization [20]. Running the model with default settings often leads to overfitting, i.e., capturing statistical noise rather than genuine ecological signals, a problem that severely undermines model transferability to future climate conditions [21]. To address this issue, researchers have developed more robust workflows. Taking studies on *Litsea cubeba* (Lour.) Pers. and *Quercus gilva* Blume as examples [22,23], three key steps are now commonly adopted: (1) prescreening environmental variables to remove multicollinearity [24]; (2) using the ENMeval package to perform a grid search over feature classes and regularization multipliers, with the optimal parameter set selected by minimizing the AICc [20]; and (3) evaluating model performance with multiple metrics, including the AUC, the true skill statistic, and Cohen's kappa [17,25]. The present study follows this optimized modeling approach to systematically investigate the ecological biogeography of *I. vestita*.

Our focal species, *Idesia polycarpa* var. *vestita* Diels (Salicaceae), is a dioecious, deciduous broadleaf tree [26,27] and an important bioenergy species in China. The natural distribution of this species is concentrated in subtropical mountainous and hilly regions, spanning the Qinba Mountains, Wuling Mountains, and the northeastern Yunnan-Guizhou Plateau, an area characterized by a typical humid subtropical monsoon climate. In recent years, the species has gained increasing attention due to its dual economic and ecological value. The fruits and seeds are rich in linoleic acid, making them high-quality raw materials for edible oil and biodiesel [28,29]. The tree grows rapidly, tolerates poor soils, and is suitable for reforesting barren hills as well as for soil and water conservation [30]. The golden autumn leaves and persistent red fruits also provide considerable ornamental value [31]. These combined advantages have led to the inclusion of this species in rural revitalization and food-oil security strategies in China. Nevertheless, research on this variety remains highly unbalanced. Downstream application-oriented studies, such as oil extraction, compositional analysis, and clonal selection, dominate the literature [32–34], while basic macroecological and biogeographic questions have received very limited attention. Specifically, the ecological niche of this species has not yet been characterized quantitatively in terms of environmental drivers [35]. The potential distribution under current climate conditions has not been systematically mapped using species distribution models, and no study has reported how the distribution might change under different emission scenarios. This knowledge gap means that decisions regarding cultivation zoning, in situ and ex situ conservation priorities lack direct scientific support, and that existing industrial layouts may face potential risks as future climate conditions evolve.

To fill these knowledge gaps, this study has three objectives: (1) to quantify the realized ecological niche of *I. vestita* by constructing an optimized MaxEnt model, identifying dominant climatic drivers and their thresholds; (2) to project current distributions onto future climate scenarios under four SSPs from BCC-CSM2-MR, revealing spatiotemporal dynamics of habitat retention, loss, and expansion; and (3) to quantify range shifts by calculating geometric centroid displacements, providing a measurable indicator of migration trajectories. Based on niche conservatism theory, we propose three testable hypotheses: (1) the

distribution is primarily governed by synergistic water-temperature interactions, with minimum temperature of the coldest month and annual precipitation as the dominant predictors; (2) future warming will cause a net habitat contraction that increases monotonically with radiative forcing; and (3) the distribution centroid will shift toward higher latitudes and elevations, with migration distance positively correlated with warming magnitude. By testing these hypotheses, this study will provide a model-based scientific foundation for industrial zoning, germplasm conservation, and climate-adaptive management of *I. vestita*.

While the MaxEnt-ENMeval pipeline has become a standard approach in species distribution modeling, the novelty of this study lies not in methodological innovation but in its first application to *I. vestita* and in three specific advances beyond conventional SDM studies: (i) quantifying actionable environmental thresholds that directly inform cultivation zoning; (ii) detecting and ecologically interpreting non-monotonic range dynamics (transient expansion followed by delayed contraction) under medium-emission pathways; and (iii) identifying long-term refugia with time-specific management recommendations (by 2030 and 2050). These contributions address critical knowledge gaps for a species of increasing bioeconomic importance.

2. Materials and methods

2.1. Acquisition and processing of species distribution data

To construct a robust occurrence dataset for *I. vestita*, we compiled species distribution records from four sources: the Chinese Virtual Herbarium (CVH, <https://www.cvh.ac.cn/index.php>, accessed 19 March 2026), the Global Biodiversity Information Facility (GBIF, <https://doi.org/10.15468/dl.8qxrfu>, accessed 20 March 2026), the China National Knowledge Infrastructure (CNKI, <https://www.cnki.net>, accessed 21 March 2026), and Google Scholar (<https://ac.scmor.com>, accessed 22 March 2026). After removing duplicate entries, an initial set of 284 occurrence points was obtained (GBIF: 135, CNKI: 107, CVH: 29, Google Scholar: 13). To mitigate the confounding effects of spatial autocorrelation on model calibration, we implemented a grid-based filtering procedure. Using ArcGIS 10.8, we overlaid a 2.5' × 2.5' grid over the study region and retained, within each grid cell, a single occurrence point nearest to the cell centroid. This approach reduces sampling bias while preserving the overall spatial extent of the species distribution. The filtering process yielded 241 high-quality occurrence records (Fig. 1), which were formatted as a comma-separated values (.csv) file for input into MaxEnt version 3.4.4 (available at http://biodiversityinformatics.amnh.org/open_source/maxent/). The base map of China used in this study was sourced from the Standard Map Service System of the Ministry of Natural Resources of China (Approval No. GS (2023)2762, accessed 22 December 2023 at <http://bzdt.ch.mnr.gov.cn/>).

2.2. Collection and screening of environmental variables

To construct the species distribution model for *I. vestita*, we initially selected 24 environmental variables across four dimensions: climate, topography, vegetation, and human activity (Table S1). Among these, 19 bioclimatic variables and elevation data were obtained from the WorldClim 2.1 database (<https://www.worldclim.org/>, accessed March 18, 2026). Slope and aspect were subsequently derived from the elevation data using ArcGIS 10.8. Vegetation cover was represented by the Normalized Difference Vegetation Index (NDVI) from the MODIS/Terra MOD13A3 product [36], and human activity intensity was quantified using the Human Footprint Index [37]. To predict future distribution patterns, we employed the BCC-CSM2-MR model, the best-performing model for climate simulation over China within the Coupled Model Intercomparison Project Phase 6 (CMIP6), and coupled this model with four Shared Socioeconomic Pathways (SSP126, SSP245, SSP370, and SSP585) to project potential distributions for the 2050s,

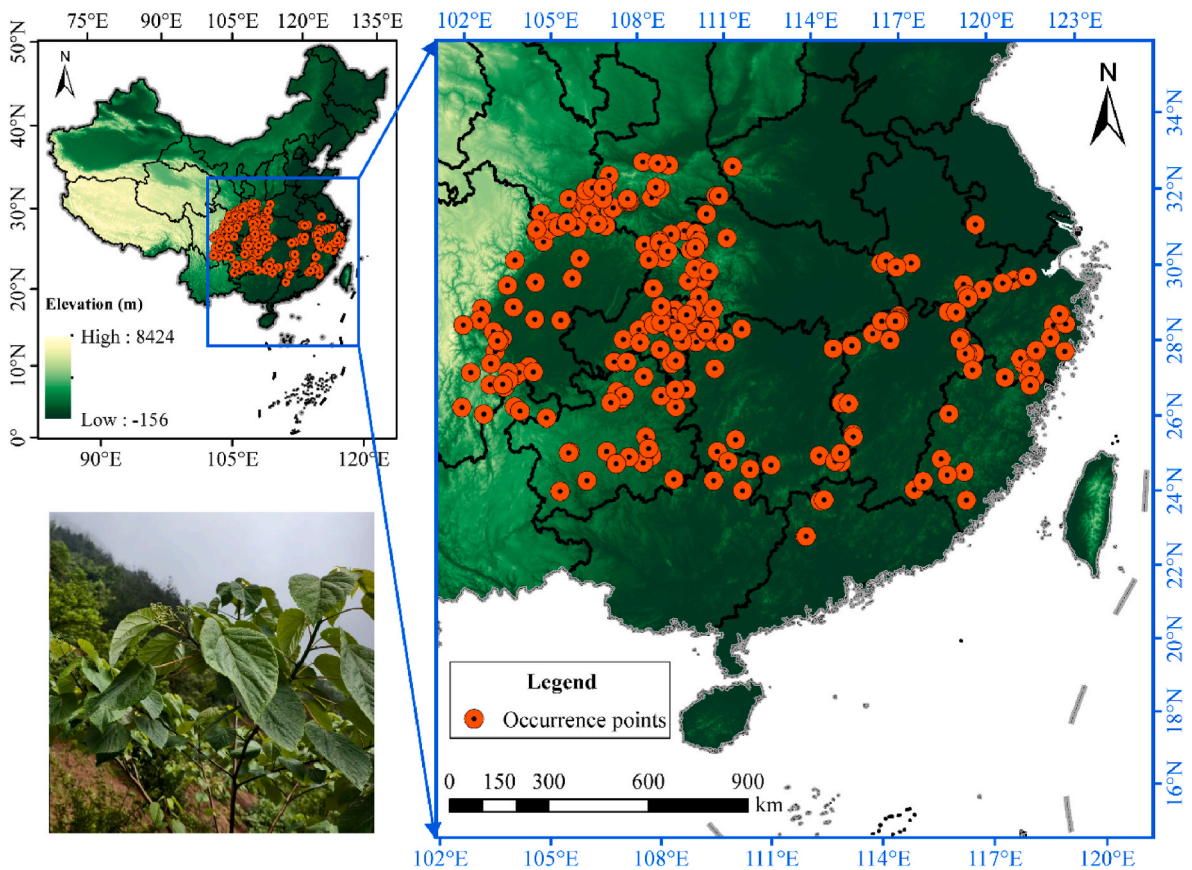


Fig. 1. Geographical distribution of the 241 recorded sites of *I. vestita* in China.

2070s, and 2090s.

To avoid overfitting and multicollinearity in MaxEnt modeling, we screened the 24 initial variables using the following procedure. Using the “Extract Multi Values to Points” function in ArcGIS 10.8, we extracted the values of the 24 environmental variables at each of the 241 occurrence points. We then performed Spearman correlation analysis in IBM SPSS Statistics 26 (Fig. 2). We set a correlation threshold of $|r| < 0.7$ as the initial retention criterion. For highly correlated variable pairs ($|r| \geq 0.7$), we retained the variable with the higher contribution rate based on preliminary MaxEnt runs (Table S1). Through this screening, we ultimately identified 10 variables that combine statistical independence with ecological significance: five climatic (Bio2, Bio4, Bio6, Bio8, Bio12), three topographic (elevation, slope, aspect), one vegetation (NDVI), and one human activity (HFI). We acknowledge that edaphic factors (e.g., soil pH, organic matter, water-holding capacity) and biotic interactions (e.g., competition, pollination) were not included due to the lack of high-resolution, spatially continuous datasets across the study region. However, at the macroscale (provincial to national level), climatic variables are widely recognized as primary determinants of plant distribution, with edaphic and biotic factors operating predominantly at local scales [38].

2.3. Optimization of MaxEnt model parameters

Feature combination (FC) and regularization multiplier (RM) are two core parameters controlling the complexity and generalizability of MaxEnt models [39]. Their optimal configuration is critical for improving the fit of species-environment relationships and enhancing the accuracy, robustness, and ecological realism of potential distribution predictions for *I. vestita*. Accordingly, we used the ENMeval 2.0.4 package [20] in R 4.2.2 to conduct a systematic grid search over the parameter space. We varied the regularization multiplier from 0.5 to

4.0 at 0.5 intervals and combined the five feature classes (linear, quadratic, product, threshold, and hinge) to generate nine feature combinations: H, HPT, L, LQ, LQH, LQHP, LQHPT, QHP, and QHPT. We determined the optimal parameter set by minimizing the corrected Akaike Information Criterion (AICc) [40].

2.4. Model calibration and performance assessment

To investigate the potential distribution patterns of *I. vestita* under future climate conditions, we developed a parameter-optimized MaxEnt modeling framework using 241 filtered and reliable occurrence records. During data preprocessing, we used stratified random sampling to split the full dataset into a training subset (75%) and a validation subset (25%), ensuring both representativeness of environmental variables and independence of statistical testing. For model settings, based on the parameter optimization results described in Section 2.3, we set the regularization multiplier to 0.5 to control model complexity and adopted the LQ feature combination to capture nonlinear species responses to environmental gradients. We introduced cross-validation to enhance internal stability, set 10000 background points to characterize the environmental background space, and ran the model 10 times with ensemble averaging of the outputs. The final output was a suitability probability raster in logistic format, providing standardized data support for multi-scenario projections and spatial visualization.

To comprehensively evaluate the predictive performance of the optimized MaxEnt model, we employed three complementary validation metrics: the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), and Cohen's kappa coefficient. The AUC quantifies the model's ability to discriminate between species occurrence points and background environmental points, with accuracy classified as follows: 0.5–0.6 indicates failed prediction, 0.6–0.7 low accuracy, 0.7–0.8 moderate accuracy, 0.8–0.9 high accuracy, and

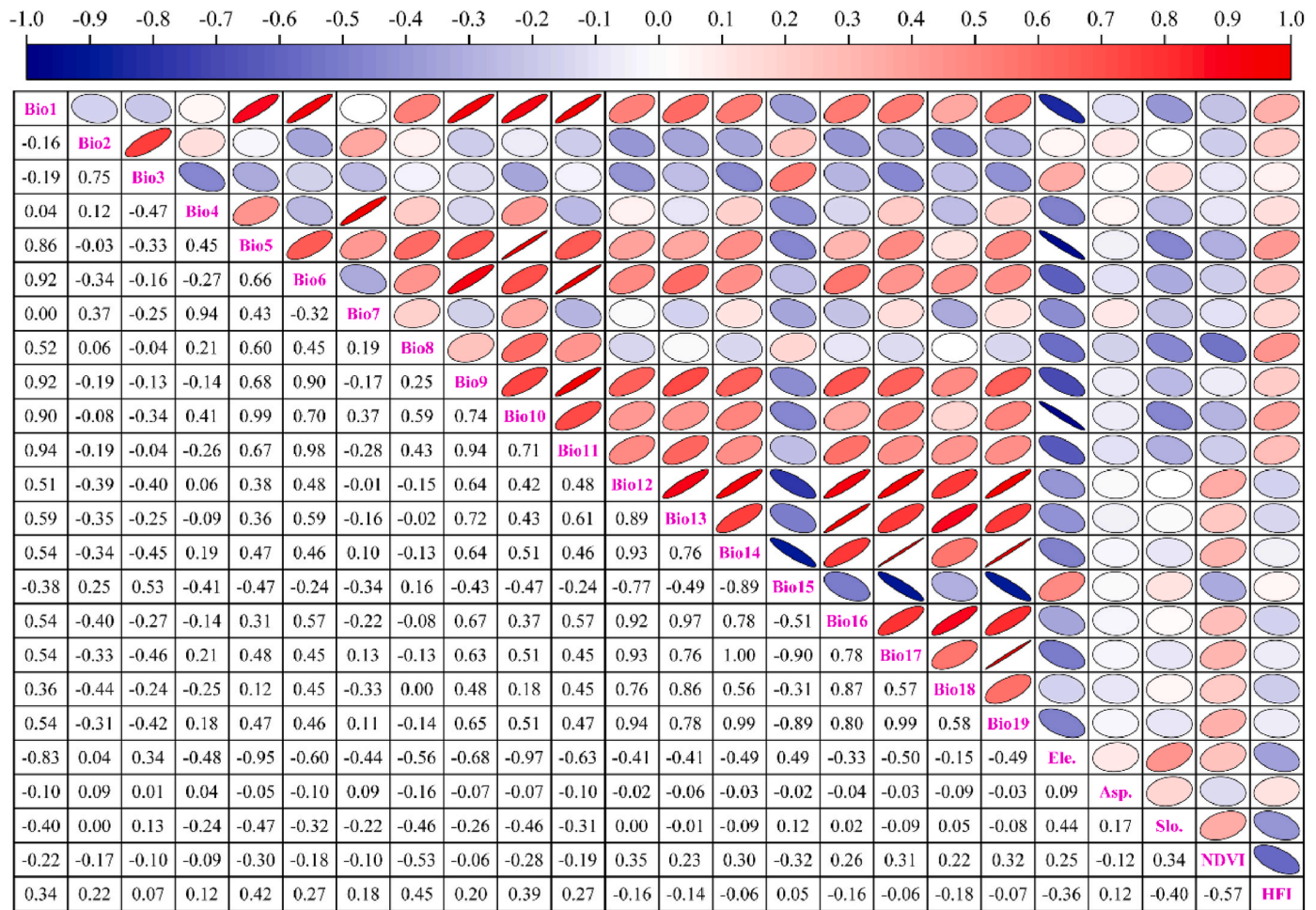


Fig. 2. Spearman correlation matrix of the initial 24 environmental variables. Ele., Asp., and Slo. stand for elevation, aspect, and slope, respectively.

0.9–1.0 excellent accuracy [41]. The TSS integrates sensitivity and specificity to correct for random biases in prediction, with the following evaluation criteria: below 0.4 indicates poor performance, 0.4–0.8 indicates good performance, and above 0.8 indicates excellent performance [42]. Cohen's kappa coefficient measures the agreement between predicted and observed classifications, ranging from -1 to 1 . A kappa value greater than 0.4 generally indicates statistically significant concordance [43].

2.5. Categorization of habitat suitability

To accurately define the potential suitable habitat boundaries for *I. vestita*, we selected the “10 percentile training presence” as the minimum probability threshold for species occurrence [44]. Based on the average habitat suitability index (P) from 10 repeated runs, this threshold was determined to be 0.0968. Following the classification criteria described above, we divided the study area into four categories: non-suitable area ($P < 0.0968$), low-suitability area ($0.0968 \leq P < 0.3$), medium-suitability area ($0.3 \leq P < 0.5$), and high-suitability area ($P \geq 0.5$) [45]. Spatial partitioning was then performed using the reclassification tool in ArcGIS 10.8.

2.6. Shifting patterns and centroid dynamics of suitable habitats

To elucidate the spatial responses of *I. vestita* to climate change, we used ArcGIS 10.8 and the mean suitability probability from 10 repeated MaxEnt runs to analyze the predicted suitable habitats from two complementary perspectives: distribution pattern dynamics and centroid

shifts. A uniform threshold of $P = 0.0968$ was applied to convert continuous probability outputs into binary distributions (1 = suitable, 0 = unsuitable) for the current climate scenario and four future SSP scenarios (SSP126, SSP245, SSP370, SSP585) across three time periods (2050s, 2070s, and 2090s). By overlaying future and current distribution boundaries, we identified three types of distributional dynamics: stable areas ($1 \rightarrow 1$), contraction areas ($1 \rightarrow 0$), and expansion areas ($0 \rightarrow 1$), thereby characterizing the direction and magnitude of shifts in spatial patterns. To quantify the overall migration trend, we calculated the geometric centroids of suitable habitats for each period using spatial statistics tools and measured centroid displacement distances and directions based on Euclidean distance. This approach provided a quantitative assessment of the range migration trajectory of the species under climate forcing.

3. Results

3.1. Model optimization and accuracy assessment

To identify the optimal parameter configuration for the MaxEnt model, we used Delta AICc as the primary metric for balancing goodness-of-fit and model complexity, with TSS as a complementary validation criterion. Under the default settings (RM = 1, FC = LQHP), the Delta AICc value reached 151.48 (Fig. 3), far exceeding the commonly accepted threshold (Delta AICc ≤ 2) in model selection. This indicates that the default parameters introduced substantial overfitting, necessitating systematic parameter tuning to enhance model reliability. Accordingly, using the ENMeval package and integrating 241

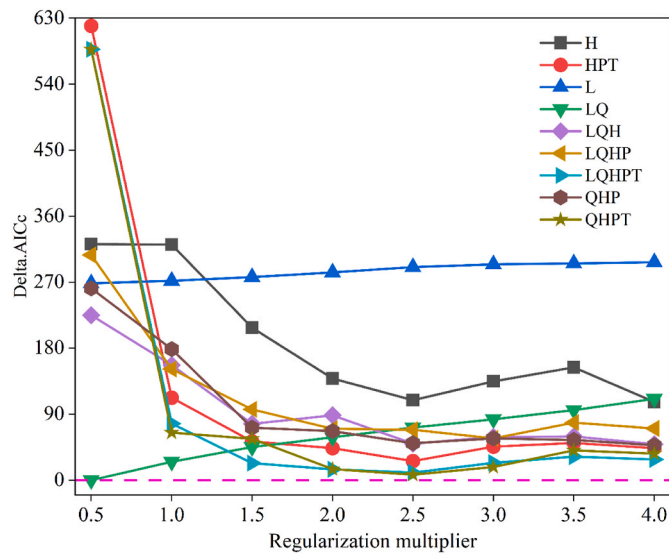


Fig. 3. Distribution of delta AICc values across nine FCs for *I. vestita*. The horizontal purple dashed line indicates the zero-reference level. FCs are represented as follows: L (Linear), Q (Quadratic), H (Hinge), P (Product), T (Threshold). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

occurrence records of *I. vestita* with 10 collinearity-filtered environmental variables, we conducted a comprehensive evaluation of multiple parameter combinations through a grid search strategy. The optimal parameter combination was $RM = 0.5$ with $FC = LQ$, yielding a Delta AICc value of 0. This indicated that the combination achieved the best trade-off between explanatory fit and predictive robustness, and that the overfitting issue was fundamentally alleviated.

In the subsequent accuracy comparison, both the default and optimized models were subjected to 10 repeated cross-validation runs. The AUC values were 0.946 for the default model (Fig. 4a) and 0.945 for the optimized model (Fig. 4b), both falling within the “excellent” category ($AUC \geq 0.9$), confirming that parameter optimization did not compromise the model's ability to capture species-environment relationships.

The slight decrease in AUC after optimization ($\Delta AUC = -0.001$) is considerably smaller than the difference in AICc between the two models ($\Delta AICc = 151.48$), reflecting that the optimized model successfully maintains core predictive performance while reducing model complexity and mitigating overfitting risk. Further accuracy assessment showed that the optimized model achieved a TSS value of 0.831. According to commonly adopted criteria, this value falls into the excellent (>0.8) category, further validating the effectiveness of the parameter optimization strategy. The kappa coefficient was 0.523, which is greater than 0.4, indicating statistically significant concordance.

3.2. Dominant environmental factors

Based on the optimized MaxEnt model, we systematically evaluated the relative importance of 10 environmental factors for the potential geographical distribution of *I. vestita* using variable contribution rates and jackknife tests. The contribution rates of environmental variables showed a clear hierarchical pattern (Fig. 5a), ranked in descending order as follows: minimum temperature of the coldest month (Bio6, 33.4%), annual precipitation (Bio12, 33.2%), temperature seasonality (Bio4, 9.6%), elevation (8.9%), mean diurnal range (Bio2, 6.0%), slope (3.6%), Human Footprint Index (HFI, 3.0%), mean temperature of the wettest quarter (Bio8, 1.5%), aspect (0.5%), and Normalized Difference Vegetation Index (NDVI, 0.3%). By factor category, climatic factors collectively contributed 83.7%, followed by topographic factors (13.0%), human activity (3.0%), and vegetation (0.3%), indicating that climatic conditions predominantly govern the species' distribution pattern at the macroscale. The regularized training gain from the jackknife test (Fig. 5b) provided complementary evidence from the perspective of individual variable importance. When used in isolation, the seven variables with the highest gain values were, in descending order, Bio6, Bio2, Bio12, Bio4, NDVI, Bio8, and elevation. Notably, NDVI and Bio8 exhibited high independent information in the jackknife test but contributed only 0.3% and 1.5%, respectively, in the full model, suggesting that the ecological information carried by these two variables was largely absorbed by other variables in the multivariate model. This highlights the complementarity between the two evaluation approaches. Based on the 85% cumulative contribution threshold, the top four variables (Bio6, Bio12, Bio4, and elevation) together accounted for 85.1%

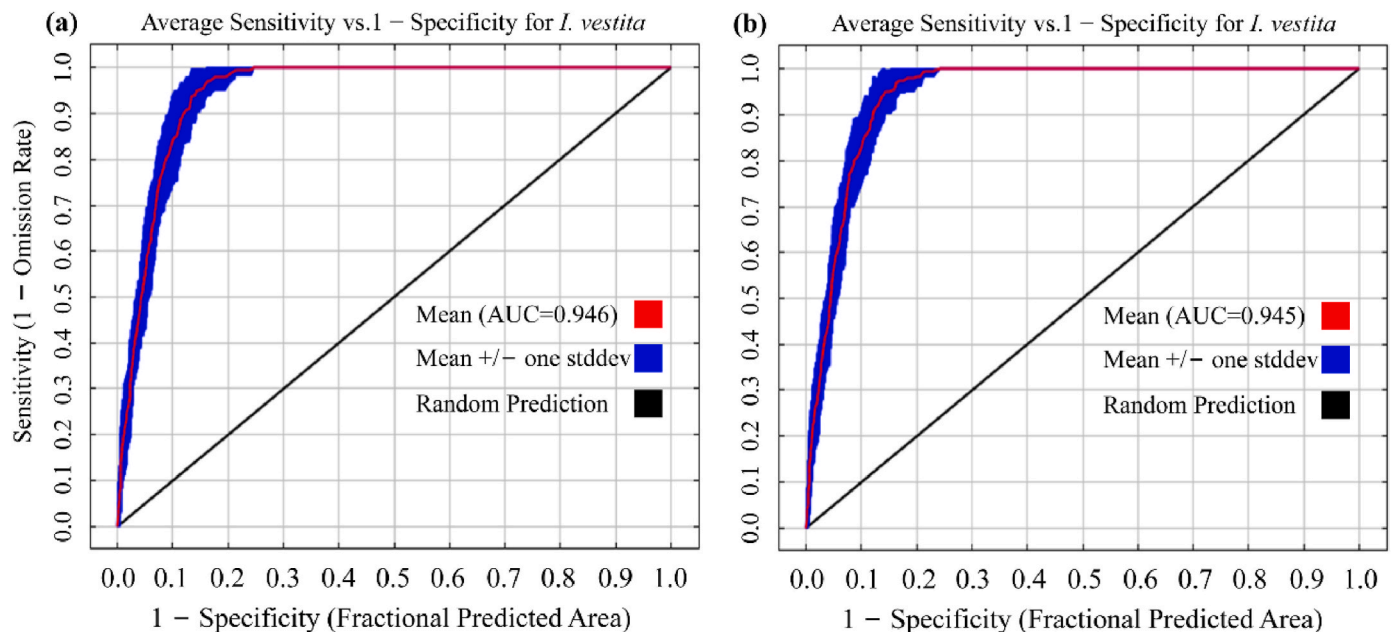


Fig. 4. Comparative analysis of the ROC curves for *I. vestita* MaxEnt model prediction accuracy, showing the AUC values using (a) default parameters versus (b) optimized parameters.

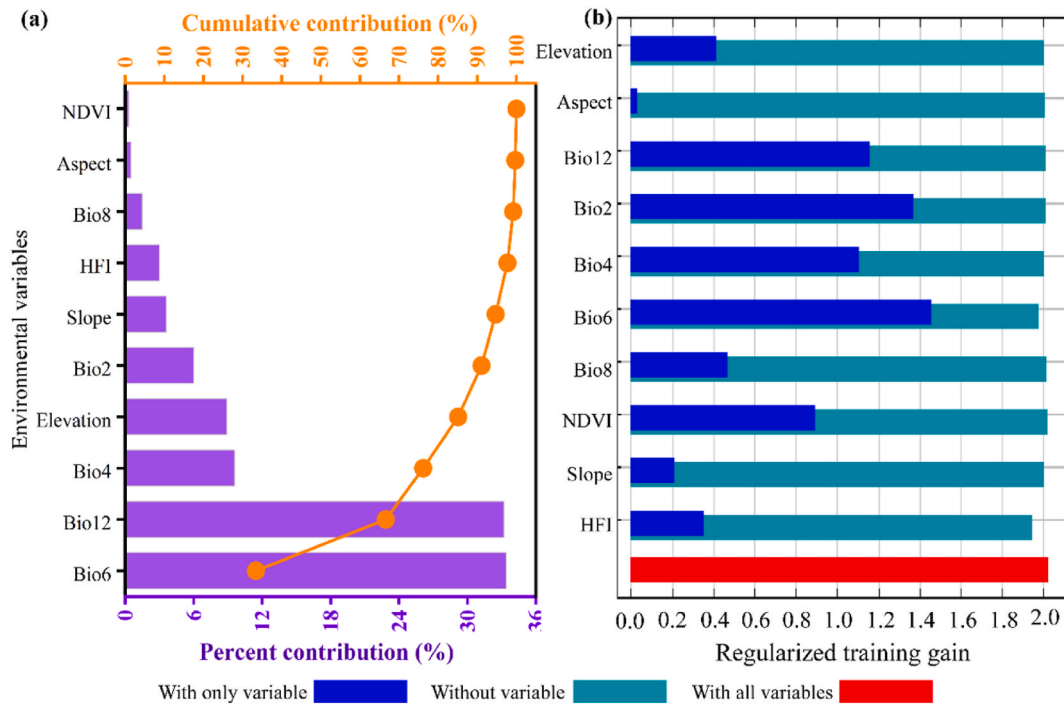


Fig. 5. Relative importance of environmental predictors for *I. vestita* in the MaxEnt model: (a) percent contribution and (b) jackknife test of regularized training gain.

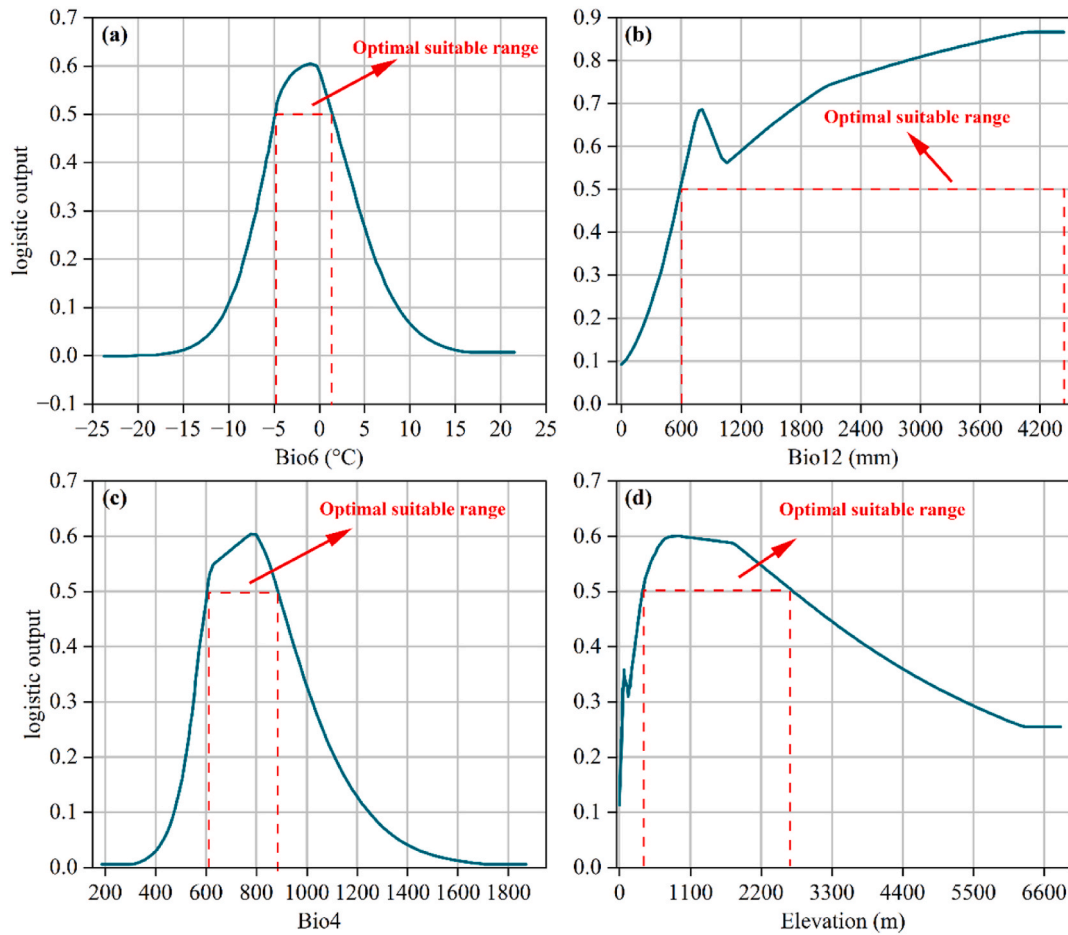


Fig. 6. Mean response curves of *I. vestita* to critical environmental variables, depicting the probability of presence (green line, mean of 10 replicates) and the optimal suitability range (red dashed lines). (a) Min temperature of coldest month (Bio6); (b) Annual precipitation (Bio12); (c) Standard deviation of temperature seasonality (Bio4); (d) Elevation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of the total contribution, jointly explaining the majority of variation in suitable habitat for this species.

To further elucidate the nonlinear effects of these dominant factors on the occurrence probability of *I. vestita*, we analyzed their individual response curves from the MaxEnt model (Fig. 6). Minimum temperature of the coldest month (Bio6, °C) exhibited a unimodal trend (Fig. 6a): the occurrence probability increased gradually from near zero at -24.52°C to 0.04 at -12.50°C , then rose sharply to a peak of 0.61 at -1.01°C , followed by a gentle decline to 0.18 at 6.60°C , after which it stabilized. Annual precipitation (Bio12, mm) showed a three-stage pattern of “slow increase, sharp increase, and saturation” (Fig. 6b): the probability increased slowly from 0.09 to 0.11 in the 0–54 mm range, then increased nearly linearly to 0.61 in the 54–698 mm range, after which the growth rate slowed, stabilizing at a high value of 0.80–0.87 at approximately 2870 mm. Temperature seasonality (Bio4, °C/100) displayed an asymmetric unimodal pattern (Fig. 6c): the probability increased gradually from 186.39 to 0.30 at 551.01, then rose sharply to a peak of 0.60 in the 551.02–798.79 range, and after passing the peak, decreased sharply first and then gently, falling below 0.01 at 1620.04. Elevation (m) showed an asymmetric bell-shaped curve (Fig. 6d). The probability first increased rapidly, forming a small local peak of 0.36 at approximately 62.98 m. After a brief fluctuation, it continued to rise, reaching a global maximum of 0.60 at approximately 818.11 m. Thereafter, the curve exhibited a two-stage decreasing pattern: the probability decreased slowly in the 818.11–1764.02 m range, then decreased more sharply in the

1764.02–6304.34 m range. Based on a suitability probability threshold of 0.5 for defining optimal habitat, the optimal environment for *I. vestita* can be characterized as: minimum temperature of the coldest month between -4.79°C and 1.46°C , annual precipitation >600 mm, temperature seasonality between 604.10 and 883.75, and elevation in the middle-low mountain belt of approximately 368.81–2646.86 m.

3.3. Potential distribution of *I. vestita* under contemporary climate conditions

Based on the MaxEnt model predictions for the current potential suitable habitat of *I. vestita* (Fig. 7), the total suitable area is approximately $141.41 \times 10^4 \text{ km}^2$, exhibiting a macro-distribution pattern broader in the east than in the west. Within this area, the low-suitability area covers $63.34 \times 10^4 \text{ km}^2$ and is the most widely distributed, spanning southeastern Tibet Autonomous Region, northwestern Yunnan, and eastern and southern China, namely Jiangxi, Fujian, Guangdong, and Guangxi. The medium-suitability area occupies $44.04 \times 10^4 \text{ km}^2$ and is concentrated in central Guizhou, eastern Sichuan, central Chongqing, southern Gansu, southern Shaanxi, northwestern Hubei, western Hunan, central Zhejiang, and southern Anhui, generally forming a discontinuous belt stretching from southwest to central to East China. The high-suitability area covers $34.03 \times 10^4 \text{ km}^2$ and is the most concentrated, highly concentrated in eastern Sichuan, northern Guizhou, eastern Chongqing, southern Gansu, southern Shaanxi, southwestern Hubei,

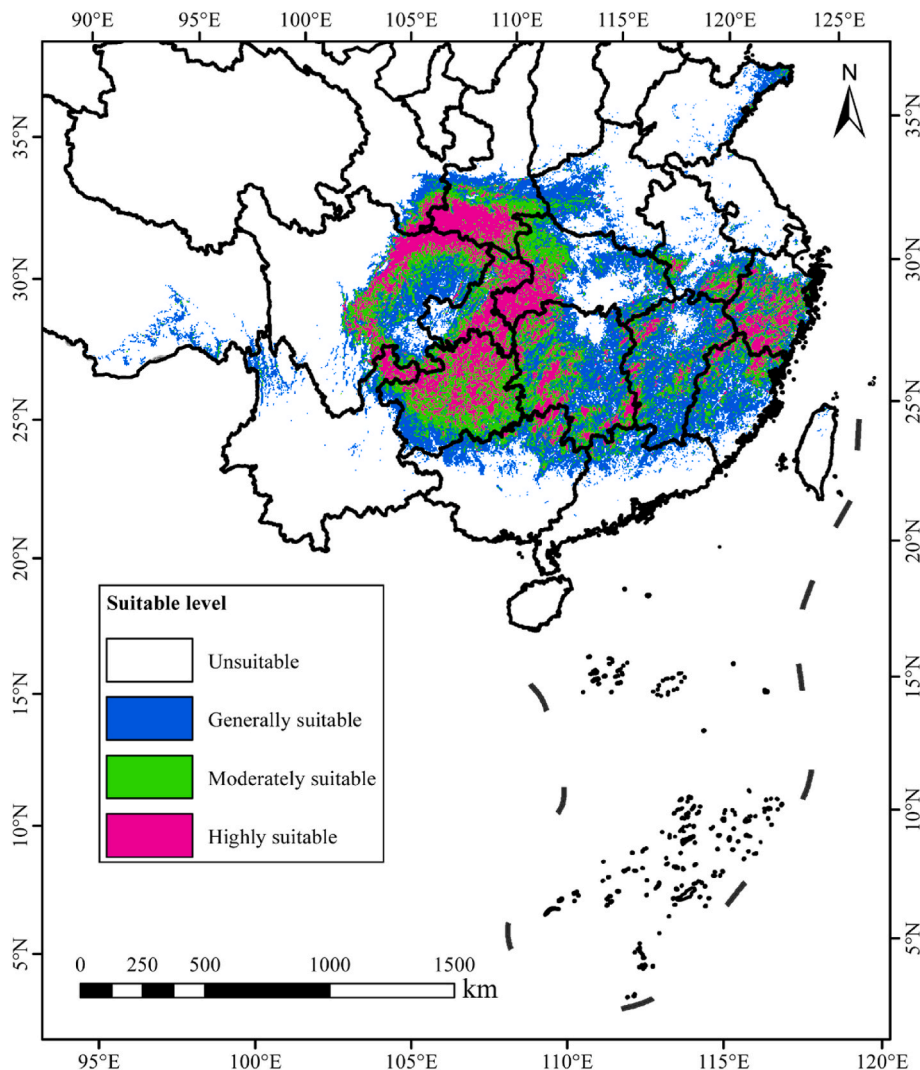


Fig. 7. Potential distribution of *I. vestita* in China under the baseline climate scenario.

western Hunan, southern Zhejiang, and southern Anhui, forming a continuous suitability core area in the Qinba Mountains and the mountainous regions of southwest China.

3.4. Future potential distribution of *I. vestita* in China under climate change scenarios

Under the SSP245 scenario, the total suitable area for *I. vestita* is projected to be $139.08 \times 10^4 \text{ km}^2$, $142.01 \times 10^4 \text{ km}^2$, and

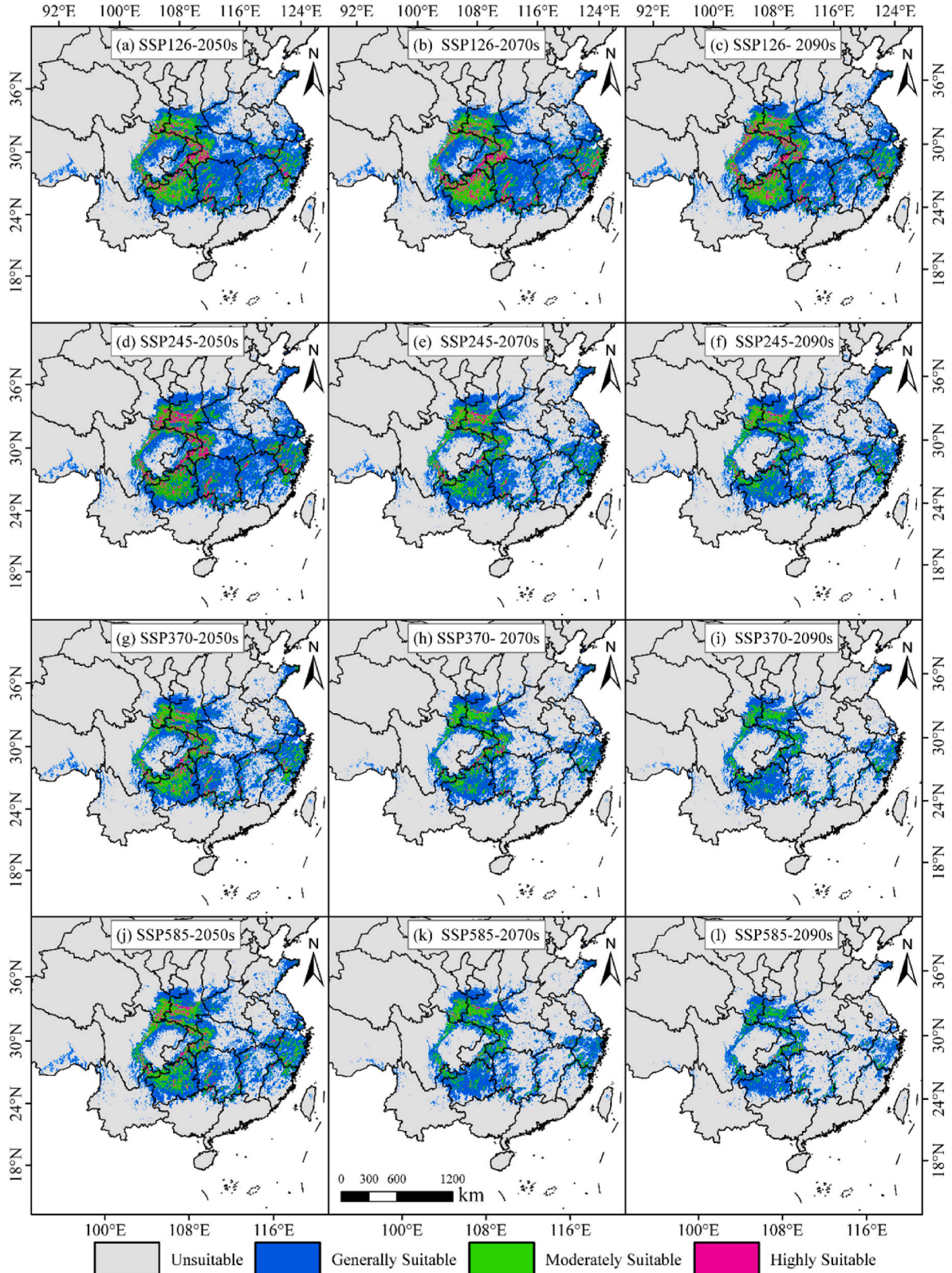


Fig. 8. Integrated projection of suitable habitat for *I. vestita* in China under future climate scenarios.

$136.39 \times 10^4 \text{ km}^2$ in the 2050s, 2070s, and 2090s, respectively, remaining relatively stable overall. The low-suitability area is the dominant type across all three periods, covering $93.12 \times 10^4 \text{ km}^2$, $91.21 \times 10^4 \text{ km}^2$, and $90.69 \times 10^4 \text{ km}^2$, respectively. The medium-suitability area accounts for $35.19 \times 10^4 \text{ km}^2$, $37.60 \times 10^4 \text{ km}^2$, and $34.32 \times 10^4 \text{ km}^2$, while the high-suitability area increases from $10.76 \times 10^4 \text{ km}^2$ to $13.20 \times 10^4 \text{ km}^2$ and then decreases to $11.38 \times 10^4 \text{ km}^2$. The spatial distribution pattern remains highly consistent across the three periods (Fig. 8a–c). The low-suitability area is continuously distributed from southeastern Tibet to East China, covering northeastern and northwestern Yunnan, eastern Sichuan, western Chongqing, southern Guizhou, southern Gansu and southern Shaanxi, southern Shanxi, western Henan, eastern Hubei, Hunan, Jiangxi, southern Anhui and southern Jiangsu, northern Zhejiang, northeastern Shandong, as well as northern Guangxi, northern Guangdong, central Fujian, and northern Taiwan. The medium-suitability area is concentrated in central Sichuan, central Guizhou, southern Gansu and southern Shaanxi, western Hubei, western Hunan, northern Fujian, southern Anhui, and southern Zhejiang. The high-suitability area exhibits a patchy distribution in central Sichuan, eastern Chongqing, western Hubei, western Hunan, western Jiangxi, and southern Zhejiang.

Under the SSP245 scenario, the total suitable area shows a continuous decline, from $148.39 \times 10^4 \text{ km}^2$ in the 2050s to $113.79 \times 10^4 \text{ km}^2$ in the 2070s, and further to $105.62 \times 10^4 \text{ km}^2$ in the 2090s. The low-suitability area decreases from $99.09 \times 10^4 \text{ km}^2$ to $81.73 \times 10^4 \text{ km}^2$ and $79.79 \times 10^4 \text{ km}^2$, yet its proportion of the total suitable area increases from 66.8% to 71.8% and 75.5%, reflecting a trend of structural concentration toward lower suitability levels under overall habitat contraction. The medium-suitability area declines steadily from $36.83 \times 10^4 \text{ km}^2$ to $22.37 \times 10^4 \text{ km}^2$, while the high-suitability area shrinks sharply from $12.47 \times 10^4 \text{ km}^2$ to $3.46 \times 10^4 \text{ km}^2$, representing a particularly pronounced loss. The spatial pattern contracts progressively over time (Fig. 8d–f). In the 2050s, the low-suitability area remains widely distributed across Southwest, Central, and East China. By the 2090s, it retreats to southeastern Tibet Autonomous Region, northeastern and northwestern Yunnan, central Sichuan, southern Guizhou, eastern Chongqing, southern Gansu and southern Shaanxi, southern Shanxi, western Henan, eastern Hubei, western Hunan, northeastern Shandong, southern Jiangsu, southern Anhui, Zhejiang, central-western Jiangxi, central Fujian, northern Guangxi, northern Guangdong, and northern Taiwan. The medium-suitability area remains stably distributed in central Sichuan, central Guizhou, southern Gansu and southern Shaanxi, eastern Chongqing, western Hubei, western Hunan, northern Fujian, and southern Zhejiang. The high-suitability area contracts to central Sichuan, southern Gansu and southern Shaanxi, eastern Chongqing, western Hubei, western Hunan, and western Jiangxi.

Under the SSP370 scenario, habitat decline is more severe than under SSP245. The total suitable area decreases from $118.22 \times 10^4 \text{ km}^2$ in the 2050s to $88.87 \times 10^4 \text{ km}^2$ in the 2070s, and further to only $76.43 \times 10^4 \text{ km}^2$ in the 2090s. The low-suitability area declines steadily from $81.29 \times 10^4 \text{ km}^2$ to $60.65 \times 10^4 \text{ km}^2$, while its proportion increases from 68.8% to 79.4%, indicating a trend toward structural simplification. The high-suitability area plummets from $6.71 \times 10^4 \text{ km}^2$ to $1.06 \times 10^4 \text{ km}^2$, nearing complete disappearance. The spatial pattern shows substantial retreat (Fig. 8g–i). In the 2050s, the low-suitability area covers southeastern Tibet Autonomous Region, northeastern and northwestern Yunnan, Sichuan, Chongqing, Guizhou, southern Gansu and southern Shaanxi, southern Shanxi, western Henan, eastern Hubei, western Hunan, northeastern Shandong, southern Jiangsu, Zhejiang, southern Anhui, central-western Jiangxi, central Fujian, northern Guangxi, northern Guangdong, and northern Taiwan. By the 2070s, the northern and eastern boundaries of the distribution area have noticeably retreated inward. In the 2090s, the medium-suitability area is concentrated in central Sichuan, eastern Chongqing, central Guizhou, southern Gansu and southern Shaanxi, western Hubei, and southern Zhejiang, while the high-suitability area persists only as fragmented patches in

western Hubei, eastern Chongqing, southwestern Hunan, and northern Guizhou.

Under the SSP585 scenario, the loss of suitable habitat is the greatest among all scenarios. The total suitable area decreases from $117.58 \times 10^4 \text{ km}^2$ in the 2050s to $83.12 \times 10^4 \text{ km}^2$ in the 2070s, and further to only $63.83 \times 10^4 \text{ km}^2$ in the 2090s. The low-suitability area declines from $82.01 \times 10^4 \text{ km}^2$ to $53.04 \times 10^4 \text{ km}^2$, while its proportion increases from 69.7% to 83.1%, indicating a highly simplified habitat structure. The high-suitability area drops from $6.44 \times 10^4 \text{ km}^2$ to $0.66 \times 10^4 \text{ km}^2$, approaching complete disappearance (Fig. 8j–l). Spatially, in the 2050s, the low-suitability area still covers southeastern Tibet Autonomous Region, northeastern and northwestern Yunnan, central Sichuan, southern Guizhou, eastern Chongqing, southern Gansu and southern Shaanxi, southern Shanxi, western Henan, eastern Hubei, western Hunan, northeastern Shandong, southern Jiangsu, Zhejiang, southern Anhui, central-western Jiangxi, central Fujian, northern Guangxi, northern Guangdong, and northern Taiwan (Fig. 8j). By the 2070s, the high-suitability area has retreated to southern Sichuan, eastern Chongqing, southern Gansu and southern Shaanxi, southwestern Hubei, and southwestern Hunan (Fig. 8k). In the 2090s, the low-suitability area further retreats to central Sichuan, southern Gansu and southern Shaanxi, eastern Chongqing, central Guizhou, western Hubei, western Hunan, western Henan, western Jiangxi, northern Fujian, Zhejiang, southern Anhui and southern Jiangsu, and northeastern Shandong. The high-suitability area persists only as scattered patches in southern Chongqing, southwestern Hubei, and southwestern Hunan (Fig. 8l).

3.5. Spatial-temporal dynamics of suitable habitats under climate change scenarios

Under the SSP126 scenario, the spatial pattern of suitable habitats for *I. vestita* is characterized by overall stability with minor adjustments. In the 2050s, the total suitable area is $159.16 \times 10^4 \text{ km}^2$, of which the stable area accounts for $120.58 \times 10^4 \text{ km}^2$ (75.76%). Relative to the current climate, the contraction and expansion areas are $20.71 \times 10^4 \text{ km}^2$ and $17.87 \times 10^4 \text{ km}^2$, with contraction and expansion rates of 13.01% and 11.23%, respectively, indicating a slight net contraction. By the 2070s, the total area slightly increases to $160.79 \times 10^4 \text{ km}^2$, with stable areas accounting for 75.71%, and contraction and expansion rates approaching balance at 12.17% and 12.12%, respectively. In the 2090s, the total area reaches $162.38 \times 10^4 \text{ km}^2$, with the proportion of stable areas decreasing to 70.17%, the contraction rate increasing to 16.83%, and the expansion rate rising to 13.00%, showing an intensified net contraction (Table 1). Spatially (Fig. 9a–c), the patterns across the three periods are similar. Stable areas are continuously distributed in Guizhou, Chongqing, Hunan, Zhejiang, Jiangxi, eastern Sichuan, southern Gansu and southern Shaanxi, western Henan, eastern and western Hubei, southern Anhui, and northern parts of South China. Contraction areas mainly occur at the southern margin of the suitable range, including eastern Sichuan, northern Guangxi, and northern Guangdong. Expansion areas are concentrated at the southeastern margin of the Qinghai-Tibet Plateau (southeastern Tibet, southern Sichuan, eastern Yunnan) and the transition zone of the Qinba Mountains-Loess Plateau (southern Gansu, southern Shaanxi, southern Shanxi), extending to northern Hunan, southern Hubei, southern Zhejiang, and northern Taiwan.

Under the SSP245 scenario, the spatial pattern shifts from net expansion in the early period to sustained net contraction in the middle and late periods, with the contraction magnitude accelerating over time. In the 2050s, the total area is $172.10 \times 10^4 \text{ km}^2$, with stable areas of $116.84 \times 10^4 \text{ km}^2$ (67.89%). The expansion area relative to the current climate is $30.82 \times 10^4 \text{ km}^2$, with an expansion rate of 17.91%, which is higher than the contraction rate of 14.20% (contraction area of $24.44 \times 10^4 \text{ km}^2$), indicating a net expansion. By the 2070s, the total area drops sharply to $158.60 \times 10^4 \text{ km}^2$, with the proportion of stable

Table 1Area changes in suitable habitat for *I. vestita* in response to various projection scenarios.

Scenario-period	Area (10 ⁴ km ²)			Rate of change (%)		
	Stability	Contraction	Expansion	Stability	Contraction	Expansion
SSP126-2050s	120.58	20.71	17.87	75.76	13.01	11.23
SSP126-2070s	121.73	19.56	19.50	75.71	12.17	12.12
SSP126-2090s	113.94	27.33	21.11	70.17	16.83	13.00
SSP245-2050s	116.84	24.44	30.82	67.89	14.20	17.91
SSP245-2070s	94.26	47.02	17.32	59.43	29.65	10.92
SSP245-2090s	85.23	56.05	17.92	53.54	35.21	11.26
SSP370-2050s	101.34	39.95	15.01	64.84	25.56	9.60
SSP370-2070s	76.31	64.97	10.64	50.23	42.77	7.00
SSP370-2090s	67.04	74.24	7.73	44.99	49.82	5.19
SSP585-2050s	99.82	41.46	16.10	63.43	26.34	10.23
SSP585-2070s	71.77	69.51	9.65	47.55	46.05	6.39
SSP585-2090s	57.69	83.57	4.60	39.55	57.30	3.15

areas plummeting to 59.43%. The contraction area expands dramatically to 47.02×10^4 km², with the contraction rate rising to 29.65%, while the expansion area decreases to 17.32×10^4 km² (10.92%), marking a shift to net contraction. In the 2090s, the total area slightly rebounds to 159.20×10^4 km², but stable areas account for only 53.54%, the contraction rate climbs to 35.21% (56.05×10^4 km²), and the expansion rate remains at 11.26% (Table 1). Spatially (Fig. 9d–f), the stable areas are significantly more contracted than under SSP126, mainly concentrated in Guizhou, Zhejiang, eastern Sichuan, southern Gansu and southern Shaanxi, and western Hubei. Contraction areas are continuously distributed in eastern Sichuan, western Chongqing, northern Guangxi, northern Guangdong, northern Fujian, and parts of Hunan, Hubei, and Jiangxi. Expansion areas are limited to southern Sichuan, northeastern Yunnan, southern Gansu and southern Shaanxi, southern Shanxi, Jiangsu, and northern Taiwan.

Under the SSP370 scenario, the suitable habitat undergoes a severe and sustained contraction process, with loss areas far exceeding newly gained areas. In the 2050s, the total area is 156.30×10^4 km², with stable areas of 101.34×10^4 km² (64.84%). The contraction area reaches 39.95×10^4 km², with a contraction rate of 25.56%, while expansion is only 15.01×10^4 km² (9.60%). By the 2070s, the total area decreases to 151.92×10^4 km², with stable areas dropping to 50.23%, the contraction area surging to 64.97×10^4 km² (contraction rate of 42.77%), and expansion shrinking to only 10.64×10^4 km² (7.00%). In the 2090s, the loss further intensifies, with the total area at 149.01×10^4 km², stable areas accounting for only 44.99%, the contraction area reaching 74.24×10^4 km² (contraction rate approaching 50%, at 49.82%), and the expansion rate falling to just 5.19% (Table 1). Spatially (Fig. 9g–i), stable areas are highly concentrated in contiguous regions including Guizhou, Zhejiang, eastern Sichuan, eastern Chongqing, southern Gansu and southern Shaanxi, western Henan, western Hubei, eastern and western Hunan and Jiangxi, and southern Anhui. Contraction areas are widespread in eastern Sichuan, western Chongqing, eastern Hubei, western Henan, central Hunan, central Jiangxi, northern Guangdong and Guangxi, and northern Fujian. Expansion areas are sporadically distributed in northeastern Yunnan, southern Gansu and southern Shaanxi, southern Shanxi, and southern Jiangsu.

Under the SSP585 scenario, the loss of suitable habitat is the greatest among all scenarios, characterized by the highest contraction rate and the lowest expansion rate. In the 2050s, the total area is 157.38×10^4 km², with stable areas of 99.82×10^4 km² (63.43%). The contraction rate reaches 26.34% (41.46×10^4 km²), while the expansion rate is 10.23% (16.10×10^4 km²), already showing net contraction. By the 2070s, the total area decreases to 150.93×10^4 km², with the proportion of stable areas plummeting to 47.55%, the contraction area surging to 69.51×10^4 km² (contraction rate of 46.05%), and the expansion rate dropping to 6.39%. In the 2090s, an extreme state is reached, with the total area at only 145.86×10^4 km², stable areas

accounting for less than 40% (39.55%), the contraction area reaching 83.57×10^4 km² (contraction rate of 57.30%), and the expansion area shrinking to just 4.60×10^4 km² (expansion rate of only 3.15%), indicating that the modeled capacity to form new suitable habitats is substantially reduced (Table 1). Spatially (Fig. 9j–l), stable areas are extremely contracted to the mountains of Guizhou, Zhejiang, southern Gansu and southern Shaanxi, eastern Sichuan, eastern Chongqing, western Hubei, and eastern and western Hunan and Jiangxi. Contraction areas continuously occupy eastern Sichuan, western Chongqing, eastern Hubei, western Henan, central Hunan, central Jiangxi, and the northern parts of coastal South China. In the 2090s, expansion areas remain only as scattered patches in southern Gansu and southern Shaanxi, southern Shanxi, and southern Jiangsu.

3.6. Centroid shifts of suitable habitats for *I. vestita* under different future scenarios

Centroid displacement analysis reveals distinct differences in the direction and magnitude of suitable habitat centroid shifts for *I. vestita* under different climate scenarios (Fig. 10). The current centroid is located in Niuchehe Town, Taoyuan County, Changde City, Hunan (110°56'E, 29°05'N). Under the SSP126 scenario, the centroid exhibits oscillatory migration. In the 2050s, it shifts approximately 65.05 km northeast to Baiyun Town, Shimen County (111°9'E, 29°38'N). In the 2070s, it moves back approximately 8.76 km southwest to Yangliupu Township, Cili County (111°7'E, 29°34'N). In the 2090s, it shifts again approximately 35.28 km northwest to Yanchi Township, Shimen County (110°58'E, 29°51'N). Under the SSP245 scenario, the centroid first migrates substantially northeastward, then shifts back southwestward. In the 2050s, it shifts approximately 121.53 km northeast to Wangjiafan Town, Yidu City, Hubei (111°21'E, 30°7'N). In the 2070s, it turns back approximately 60.76 km southwest to Wufeng Town, Wufeng Tujia Autonomous County (110°44'E, 30°5'N). In the 2090s, it advances again approximately 35.41 km northeast to Duzhenwan Town, Changyang Tujia Autonomous County (110°53'E, 30°23'N). Under the SSP370 scenario, the centroid shows a sustained northwestward migration trend, with a slight southward deviation in the later period. In the 2050s, it shifts approximately 92.21 km northwest to Suojie Township, Shimen County (110°51'E, 29°54'N). In the 2070s, it continues to migrate approximately 58.81 km northwest to Niuzhuang Township, Wufeng County (110°24'E, 30°16'N). In the 2090s, it deflects approximately 54.69 km southwest to Zhongying Town, Hefeng County (109°57'E, 29°57'N). Under the SSP585 scenario, the migration trajectory is similar to that under SSP370, showing progressive displacement. In the 2050s, it shifts approximately 100.11 km northwest to Hupingshan Town, Shimen County (110°46'E, 29°58'N). In the 2070s, it continues to migrate approximately 59.89 km northwest to Wuyang Township, Hefeng County (110°11'E, 30°10'N). In the 2090s, it shifts approximately 17.35 km southwest to Zhongying Town, Hefeng County

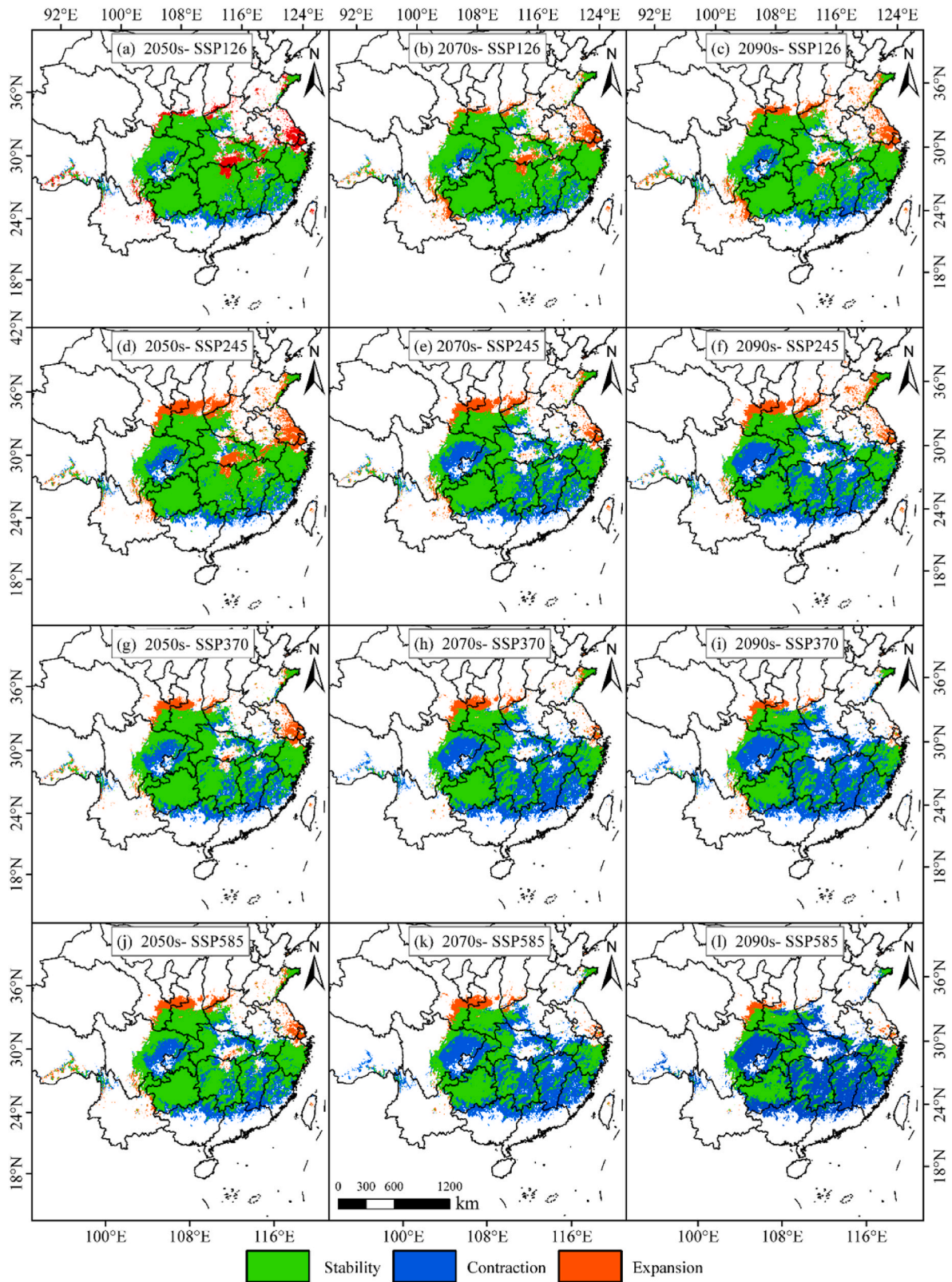


Fig. 9. Changes in stable, lost, and gained areas of *I. vestita* distribution under different climate change scenarios.

(110°2'E, 30°5'N).

4. Discussion

4.1. Model calibration and performance assessment for *I. vestita*

The reliability of species distribution models largely depends on the

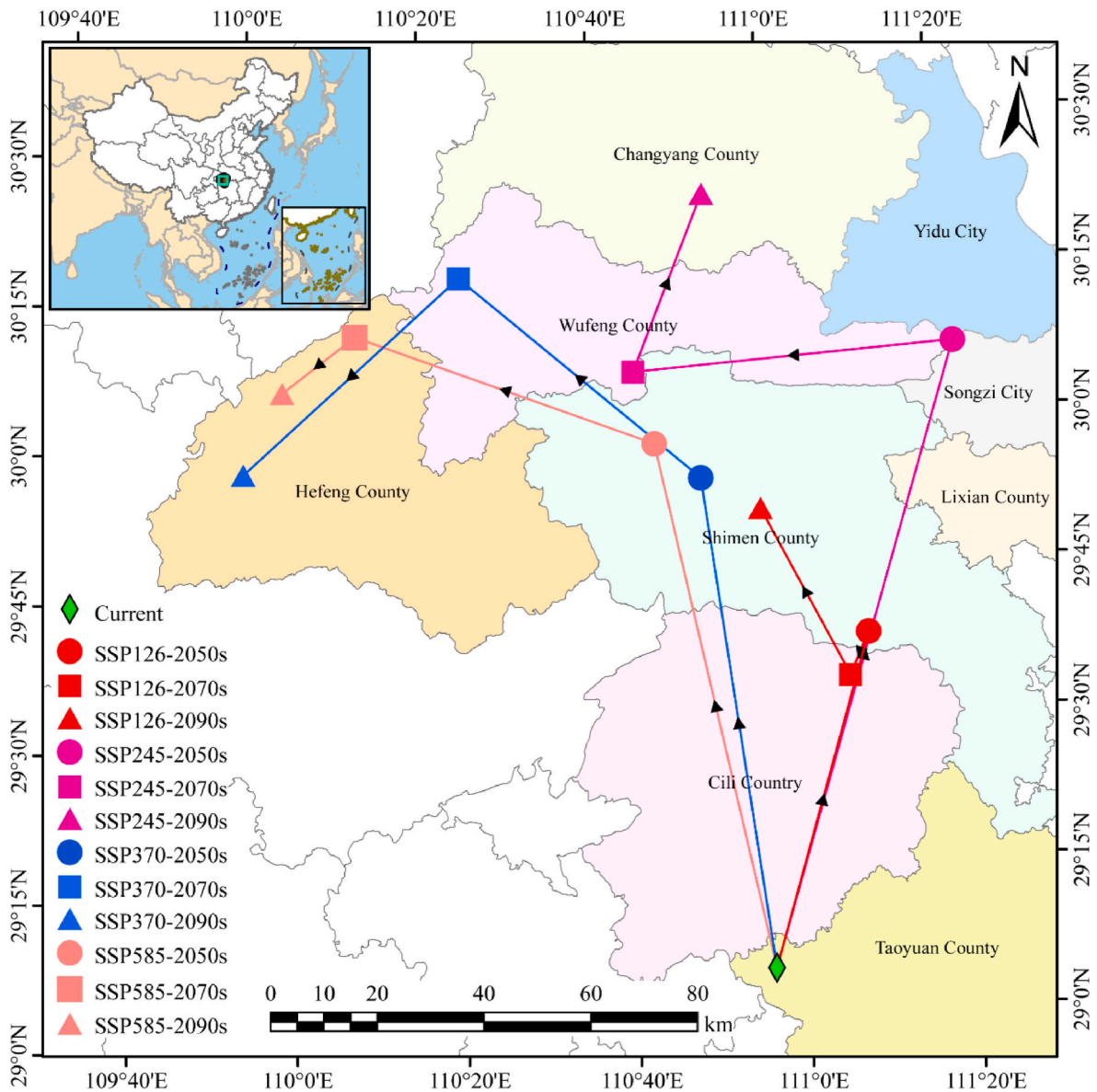


Fig. 10. Centroid migration pathways of *I. vestita* under different climate scenarios.

quality of parameter tuning. Default settings often introduce excessive model complexity, misinterpreting random noise in training data as genuine ecological signals, thereby weakening the model's ability to extrapolate to future climate conditions [21,46,47]. In this study, the Delta AICc value under default parameters was as high as 151.48, far exceeding acceptable levels of model fit. After conducting a grid search over regularization multipliers and feature combinations using the ENMeval package, the Delta AICc value dropped to zero, and the final model was validated by both AUC (0.945) and TSS (0.831) for its robustness in predicting the distribution of *I. vestita*. This finding supports a fundamental principle in species distribution modeling: extrapolation bias caused by overparameterization is often more concerning than the uncertainty inherent in climate models themselves, and minimizing AICc serves as an effective criterion for selecting parameters that enhance the transferability of niche models to future climate conditions [48,49]. In terms of modeling workflow, the optimization procedures employed in this study do not depend on the unique attributes of this species and are therefore equally applicable to predicting the distributions of other subtropical native tree species.

Examining the model structure in light of the optimization results

provides a clearer understanding of how *I. vestita* responds to environmental factors. The optimal model required only linear (L) and quadratic (Q) feature classes to adequately capture the species' distribution pattern, indicating that although the responses do not strictly follow linear relationships, their overall shape is smooth, without the complex fluctuations of multiple peaks or threshold jumps. This is inherently consistent with the species' broad ecological amplitude as a widely distributed native tree species. Previous studies have shown that models with simple feature combinations tend to exhibit stronger extrapolation robustness under climate change, whereas overly complex models tend to solidify spurious correlations in training data as apparent ecological laws [50]. For this reason, model selection should not rely solely on AUC, as unusually high AUC values often signal overfitting [51]. The performance of the various evaluation metrics in this study supports this view: both AUC and TSS reached excellent levels, and although Kappa was somewhat lower (0.523), this discrepancy itself is consistent with the known systematic influence of species prevalence on the Kappa statistic [52]. Overall, the optimized model does not sacrifice goodness-of-fit for simplicity but instead achieves a balance between statistical accuracy and ecological realism, thereby supporting the

reliability of the subsequent multi-scenario predictions.

4.2. Dominant environmental factors controlling the distribution of *I. vestita*

Minimum temperature of the coldest month (Bio6) and annual precipitation (Bio12) together contributed 66.6% of the model's explanatory power. These two variables alone captured the core constraints defining the species' distributional boundaries, with Bio6 governing temperature filtering along the north–south axis and Bio12 regulating moisture availability gradients along the east–west axis. The response curve for Bio6 formed a steep suitability peak between -4.79°C and 1.46°C , dropping sharply on both sides. This nearly symmetric unimodal shape indicates the presence of qualitatively different stress factors on either side of the optimal range. On the low-temperature side, the constraint mechanism of extreme winter cold extends beyond outright freeze damage, as the persistent suppression of growth and reproductive performance by sublethal temperatures also constitutes a critical limitation [53,54]. The constraint on the warm-winter side is more subtle, because insufficient effective chilling can disrupt bud dormancy release, thereby impairing the precise coupling between spring leaf-out and local climatic rhythms [55,56]. Thus, Bio6 carries a dual ecological signal. It defines both the lower limit of extreme cold tolerance and indicates that excessive winter warming is not beneficial for this species. This latter constraint is a type of stress easily overlooked in climate warming research. The response curve for Bio12 crossed the suitability probability threshold at approximately 600 mm of annual precipitation and remained high above 2000 mm, reflecting the species' dependence on humid subtropical mountain climates.

Elevation and temperature seasonality (Bio4) further delineate the three-dimensional structure of suitable habitats. The unimodal shape of Bio4 excludes the continental interior with strongly fluctuating seasonal temperatures, consistent with the theoretical expectation of the climatic variability filtering hypothesis, which states that species with relatively narrow niche breadths are systematically excluded from highly variable environments [57]. The elevation response followed a bell-shaped curve, with low-elevation heat and high-elevation cold imposing constraints from both directions, restricting the suitable range to low- and mid-elevation mountain belts. The independent contributions of NDVI and the Human Footprint Index together amounted to less than 4%. This result does not negate the ecological effects of anthropogenic disturbance, for which ample evidence exists regarding the destructive impacts of logging and land-use change at local scales. Instead, it reveals that at the biogeographic scale, climatic filters play a more fundamental role than local human activities in determining species' macro-distributional boundaries [58]. The contribution of topographic factors was similarly limited, which more likely reflects that their redistribution effects on water and heat conditions are statistically absorbed by the main climatic effects, rather than indicating a lack of ecological significance for topography itself [59,60].

Integrating the thresholds of all factors, the ideal habitat for *I. vestita* can be characterized as low-to mid-elevation humid mountain areas with mild winters (Bio6: -4.79°C to 1.46°C), abundant annual precipitation exceeding 600 mm, moderate seasonal temperature fluctuations (Bio4: 604.10 – 883.75), and moderate elevation (368.81–2646.86 m). This niche profile closely aligns with results from studies on dominant tree species in the subtropical evergreen–deciduous broadleaf mixed forests of China, collectively pointing to a macroecological pattern in which minimum thresholds of heat and moisture define the core boundaries, while topography plays a secondary regulatory role through local redistribution of water and heat [61]. Given that increasing precipitation variability under future climate scenarios is increasingly surpassing temperature change itself in its impact on species' distributional boundaries, the quantification of the lower threshold of Bio12 provides direct reference value for long-term climate risk assessment in production areas [62].

Physiologically, the Bio6 optimum (-4.79°C to 1.46°C) aligns with frost tolerance limits and chilling requirements for bud dormancy release [63]. The Bio12 threshold (>600 mm) corresponds to minimum water availability to avoid drought-induced hydraulic failure [64]. The elevation optimum (369–2647 m) reflects trade-offs between temperature maxima and growing season length [65].

4.3. Spatiotemporal patterns of suitable habitats for *I. vestita* under climate change scenarios

The response patterns of suitable habitats for *I. vestita* under different emission pathways show fundamental differences that cannot be summarized simply as area contraction. Under the low-emission SSP126 scenario, the total suitable area remains largely stable throughout the 21st century, with even a slight expansion in the 2070s, indicating that if global warming is limited to 1.5 – 2.0°C , the core of the species' current distribution is likely to be maintained [66]. However, starting from the SSP245 scenario, the trend shifts markedly: the total suitable area contracts continuously, and the high-suitability area nearly disappears by the 2090s under the SSP370 and SSP585 scenarios. Particularly noteworthy is the brief expansion of suitable area in the 2050s under the SSP245 pathway before shifting to severe contraction. This “early increase followed by later decrease” trajectory closely aligns with the adaptive lag characteristics of long-lived woody perennials. Because trees have long generation times and low migration rates, they often exhibit short-term physiological compensation in response to initial warming, and only when environmental thresholds are imperceptibly crossed does a delayed range collapse occur [67,68]. Therefore, inferring species persistence solely from instantaneous climate suitability while neglecting ecological processes such as dispersal limitation and demographic lag would overestimate the actual capacity of species to survive under climate change [69,70]. The short-term expansion of suitable habitat observed for *I. vestita* under the medium-emission pathway may be interpreted as consistent with an adaptive lag response prior to potential population decline. However, we caution that this interpretation remains speculative, as correlative niche models assume equilibrium between species and their environment, and the observed pattern could alternatively arise from equilibrium assumption artifacts rather than genuine demographic delay [67]. Testing the adaptive lag hypothesis would require integrating dispersal kernels, demographic modeling, genetic diversity gradients, or empirical phenological data, which are currently unavailable for this species. We therefore present this interpretation as hypothesis-generating rather than confirmatory, and encourage future studies to collect the necessary data for rigorous validation.

Spatially, newly gained suitable areas repeatedly appear in the Qinba Mountains, the southeastern margin of the Qinghai-Tibet Plateau, and the transitional zone of the Loess Plateau, whereas lost areas are continuously distributed at the southern margin and low-elevation belt of the current distribution range. The distribution centroid tends to shift persistently from Niuchehe Town in Hunan toward the Wuling Mountain–Wushan Mountain range in western Hubei, with the magnitude of migration increasing with radiative forcing. The bidirectional poleward and upward range shift driven by climate warming is a well-recognized principle in macroecology, and this study adds new evidence for a subtropical woody oilseed species [1,71]. However, hidden beneath the directionality of the centroid shift is a more profound ecological risk: stable areas are highly concentrated in the Qinba Mountains and the mountainous regions of southwest China, whereas lost areas are expanding outward in a continuous pattern. This spatial divergence signals that suitable habitats are undergoing severe fragmentation. Previous studies have demonstrated that climate-driven habitat fragmentation, by disrupting gene flow, reducing metapopulation recolonization probabilities, and exacerbating edge effects, can have ecological and evolutionary consequences as severe as the total loss of habitat area itself. The remaining populations may further face

cascading risks of reduced genetic diversity and diminished recovery resilience [72,73].

We acknowledge that centroid migration analysis simplifies complex spatial dynamics by reducing multidimensional fragmentation to a single point movement. It does not account for landscape connectivity, land-use change, or patch isolation [74]. However, our analysis of stable, lost, and gained areas (Fig. 9) reveals intensifying fragmentation, which can disrupt gene flow and reduce metapopulation persistence [72]. Future studies should incorporate circuit theory [75] or least-cost path analysis to better represent dispersal corridors and barriers.

The spatial patterns and fragmentation trends described above have direct implications for the industrial planning and germplasm conservation of *I. vestita*. The existing continuous distribution belt in the Qinba Mountains and Wuling Mountains may disintegrate under high-emission pathways into multiple mountain isolates separated by unsuitable matrix, posing fundamental challenges to in situ conservation of germplasm resources. This finding is corroborated by recent parallel studies, which have shown that suitable habitats for multiple subtropical woody oilseed species in China exhibit a convergent pattern of shifting toward higher elevations and higher latitudes under climate change, with low-elevation populations at the southern margin of current distributions facing extensive loss risks [22,76]. These independent lines of evidence collectively indicate that subtropical woody bioenergy plants in China, as a group, are under pressure from rapid climate gradient shifts. Accordingly, this study recommends that the Qinba Mountains and other core suitable areas be prioritized as strategic regions for in situ germplasm conservation and collection of superior provenances. Meanwhile, current plantation areas distributed at the southern margin with high climate risk should be gradually adjusted westward to western Hubei and eastern Chongqing, which are projected to remain highly suitable in the future, as part of long-term planning [77,78].

4.4. Conceptual and applied advancements of this study

Beyond the routine application of MaxEnt-ENMeval, this study offers three specific advancements. First, unlike many SDM studies that stop at identifying dominant variables, we provide quantifiable thresholds (e.g., Bio6: -4.79°C to 1.46°C ; Bio12: >600 mm; elevation: 369–2647 m) that can directly guide field-based provenance selection and plantation zoning. Second, the non-monotonic trajectory under SSP245, expanding in the 2050s before contracting thereafter, is interpreted as a pattern consistent with the adaptive lag hypothesis in long-lived woody perennials, a demographic mechanism rarely addressed in correlative SDM studies. We acknowledge that this interpretation remains hypothesis-generating and requires validation with demographic, genetic, and dispersal data in future studies. Third, the identification of the Qinba and Wuling Mountains as persistent refugia, combined with explicit time horizons (germplasm collection by 2030; phased withdrawal from southern margins by 2050), translates model projections into actionable management timelines.

4.5. Model robustness and parameter uncertainty

While we did not perform a post-hoc sensitivity analysis across varying parameter combinations, the ENMeval optimization procedure systematically evaluated 72 candidate models (9 feature class combinations $\times$ 8 regularization multipliers from 0.5 to 8.0). The optimal model (RM = 0.5, FC = LQ) was selected by minimizing AICc, a criterion known to balance goodness-of-fit against overfitting. Models with alternative parameters, such as the default settings (RM = 1.0, FC = LQHP), produced Delta AICc values exceeding 150, indicating substantially inferior statistical support. This clear separation between the optimal and suboptimal parameter space suggests that our core findings, particularly the identification of the Qinba and Wuling Mountains as persistent refugia, are not arbitrary artifacts of parameter choice. Furthermore, the spatial congruence between these predicted

refugia and independently documented healthy natural populations provides empirical corroboration.

We acknowledge that a formal sensitivity analysis mapping refugia locations across parameter combinations was not performed. However, the optimal model was clearly distinguished from suboptimal models, and our core refugia align with independent field observations. A formal sensitivity analysis would further clarify structural stability and is recommended for future studies.

4.6. Limitations regarding edaphic and biotic predictors

We acknowledge several limitations. First, edaphic factors (including groundwater availability) and competitive interactions were not included. Climatically suitable areas with poor soils or limited groundwater may be overestimated, whereas microtopographic refugia may be underestimated. Competition may limit colonization of suitable areas, particularly in mountainous terrain where edaphic factors mediate range shifts. Future studies should integrate soil and groundwater data alongside species interaction metrics. Second, using a single GCM (BCC-CSM2-MR) does not account for inter-model uncertainty. While this model is best-performing for China, other GCMs may produce divergent projections. Given its moderate warming tendency, our predicted habitat contraction may be conservative, and the SSP245 transient expansion might vary across models. Future multi-model ensemble studies are needed. Third, the 10th percentile training presence rule is sensitive to sampling bias and spatial clustering. We adopted this common threshold for comparability, but alternative thresholds or continuous indices could alter class boundaries. We therefore caution against relying solely on discrete classes and recommend future evaluations of multiple thresholding methods. Fourth, beyond 2.5' grid filtering, we did not implement spatial block cross-validation or environmental dissimilarity metrics. Residual spatial autocorrelation may overestimate model transferability to novel climates. Future studies should adopt spatially structured cross-validation to address this limitation. Fifth, our projections focus on three periods (2050s, 2070s, 2090s) at 20-year intervals. While aligned with CMIP6 standards, this resolution may miss tipping points or transient suitability windows critical for forestry planning. Decadal interpolation or continuous time-series projections are recommended for future studies to better resolve such dynamics. Sixth, our conservation priorities lack population genetic data and landscape connectivity metrics. Climatically stable refugia with high adaptive genetic diversity should ideally be prioritized as evolutionary reservoirs, but such data are unavailable for *I. vestita*. Future studies integrating population genomics and landscape genetics are recommended.

4.7. Caveats of correlative niche modeling under non-analog climates

We recognize that our MaxEnt model assumes equilibrium between species distributions and their environment, an assumption that becomes problematic under non-analog future climates where extrapolation beyond training data can produce unreliable predictions [79]. Our projections also assume niche conservatism, yet if *I. vestita* possesses adaptive capacity or phenotypic plasticity, its fundamental niche could shift, potentially mitigating the predicted habitat contraction [68]. Additionally, biotic interactions (e.g., competition, pollination) were excluded but may facilitate or constrain range shifts [67], and evolutionary adaptation over multi-decadal timescales could alter the realized niche, though long-lived trees have limited capacity for rapid evolution [73].

Furthermore, our spatial overlap analysis does not consider climate velocity, topographic complexity, or protected area networks. These factors could substantially facilitate or hinder natural migration of this dioecious, wind- or animal-dispersed tree species. Climate velocity may exceed colonization capacity in some areas [80], while topographic complexity can create microclimatic refugia [81]. Future studies

integrating these factors are needed to better assess natural migration potential.

We therefore caution that our projections represent climate-driven potential distributions under equilibrium assumptions, not deterministic forecasts, and should be interpreted as hypotheses requiring empirical validation.

5. Conclusion

This study provides the first quantitative characterization of the ecological niche and climate driven habitat dynamics of *I. vestita*, closing a critical knowledge gap for this bioenergy tree. Our results confirm that hydrothermal factors, most notably minimum temperature of the coldest month (Bio6) and annual precipitation (Bio12), synergistically govern its distributional boundaries, constraining optimal habitats to mild, humid, mid to low elevation zones. Future projections reveal divergent trajectories. Under the low emission SSP126 scenario, suitable habitats remain largely stable throughout the 21st century. In contrast, under SSP370 and SSP585, suitable habitats undergo severe contraction, with highly suitable areas nearly disappearing by the 2090s. The rise and fall pattern under SSP245, characterized by transient expansion followed by delayed contraction, exemplifies adaptive lag in long lived trees and cautions against interpreting short term gains as long term resilience. Spatially, the Qinba and Wuling Mountains emerge as persistent refugia, whereas southern low elevation populations face progressive decline. These findings carry actionable implications. Based on these model projections, as a preliminary guideline, we suggest prioritizing these refugia for in situ germplasm preservation while gradually relocating plantations from climatically vulnerable southern margins toward western Hubei and eastern Chongqing. However, socio-economic, institutional, and genetic feasibility assessments are needed before implementation. Specifically, germplasm collection and introduction trials in the eastern Chongqing high suitability zone should be completed by 2030, followed by a phased withdrawal from high-risk southern margins such as northern Guangdong and Guangxi by 2050. Methodologically, this study reaffirms that rigorous parameter optimization is indispensable for model transferability under future climate scenarios. Overall, this work delivers an evidence-based framework to guide climate-resilient planning and conservation of *I. vestita*. However, application of these results at local scales should integrate complementary edaphic and biotic assessments, as these factors were not explicitly modeled.

CRediT authorship contribution statement

Yixuan Peng: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Longcheng Jiang:** Conceptualization, Data curation, Validation, Writing – review & editing. **Jin Wang:** Conceptualization, Data curation, Methodology, Validation, Writing – review & editing. **Rou Ma:** Conceptualization, Data curation, Validation, Writing – review & editing. **Hua Lin:** Formal analysis, Validation, Writing – review & editing. **Evgeny Lopatin:** Conceptualization, Writing – review & editing. **Yangzhou Xiang:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Supervision, Validation, Visualization, Writing – review & editing. **Hongyan Yang:** Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – review & editing. **Yuan Li:** Conceptualization, Methodology, Resources, Visualization, Writing – review & editing.

Conflicts of interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biombioe.2026.109889>.

Data availability

Data will be made available on request.

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