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Ensemble species distribution modeling and InVEST-based habitat quality assessment for Cupressus funebris under climate change: identifying refugia, ecological security patterns, and conservation priorities in China

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Research Article

Keywords: BIOMOD2, climate change, Cupressus funebris, ecological security pattern

Posted Date: November 11th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11012365/v1

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Additional Declarations: No competing interests reported.

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Funding:

This research was funded by Science Research Project of Hebei Education Department (BJK2023104).

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Abstract

Cupressus funebris, an indigenous and ecologically important conifer in China, is increasingly endangered by climate change and habitat fragmentation. Using an ensemble species distribution model (BIOMOD2), we projected current and future habitat suitability under three climate

scenarios (SSP1-2.6, SSP2-4.5, SSP5-8.5) for the 2050s, 2070s, and 2090s. We integrated 355 occurrence records and bioclimatic variables using 12 algorithms. We also used the InVEST Habitat Quality model to assess current habitat quality and degradation, and constructed an ecological security pattern from habitat patches and resistance surfaces. This framework identified climate refugia and priority conservation zones. Random Forest performed best (AUC = 0.92 ± 0.02, TSS = 0.85 ± 0.03). Temperature seasonality (Bio04) and minimum temperature of the coldest month (Bio06) were the main climatic drivers. Results show severe range contractions under all scenarios: habitat loss ranges from –28.5% (SSP1-2.6) to –62.4% (SSP5-8.5) by the 2090s, with elevational shifts of 180–310 m. Persistent climate refugia (about 15,200 km²) occur in topographically complex regions like the Hengduan Mountains and Northern Yunnan. InVEST showed that high-quality habitat patches are largely restricted to these refugia, while degradation hotspots overlap with projected climate loss zones. A spatial conservation priority map combining climate suitability and habitat quality guides adaptive management, highlighting areas for immediate protection, assisted migration, ex situ conservation, and ecological restoration. This multi-model framework supports climate-resilient conservation strategies for *C. funebris*.

Keywords: BIOMOD2, climate change, *Cupressus funebris*, ecological security pattern

InVEST,

INTRODUCTION

Temperate coniferous forests in China are undergoing progressive pressure from a combination of rapid climate change, habitat fragmentation, and the expansion of human activities[1,2]. These combined threats pose significant risks to native conifer species. many of which are highly sensitive to shifts in temperature and precipitation regimes. In particular, endemic species with limited and fragmented natural ranges are increasingly vulnerable to environmental change and anthropogenic disturbance, wich underscore the urgent need for proactive conservation planning.

Among these species, *Cupressus funebris*, commonly known as the Chinese Weeping Cypress, is of particular concern because its natural distribution is both limited and fragmented, despite its widespread cultivation as an ornamental and timber tree[3,4]. This species is endemic to central and parts of Southern China, and extends a bit into Northern Vietnam. It has long been valued for its durable wood and the production of fragrant cedarwood oil, making it a species of cultural and economic importance[4]. However, natural populations of this conifer are increasingly threatened by habitat loss, land-use change, and uncertain future climatic conditions[5]. Then, understanding the potential changes in the species geographic distribution is crucial for conservation planning.

Species Distribution Modeling (SDM) provides a strong framework not only for understanding the relationships between species occurrences and environmental variables, but also for predicting suitable habitats under current and future climates[6,7]. Among various SDM platforms, BIOMOD2 has become a widely used R package because it integrates multiple modeling algorithms, such as Maxent, Random Forest, and Generalized Linear Models into an ensemble forecasting approach, which reduces the uncertainty due to single-model predictions[8,9]. By combining occurrence records of *C. funebris* with high-resolution bioclimatic and topographic variables, BIOMOD2 can generate probabilistic maps of current and future habitat suitability. It offers valuable insights into the potential range dynamics of this species under different climate scenarios. Recent studies applying BIOMOD2 to *C. funebris* indicate that its current suitable habitat is mainly concentrated in the subtropical and warm-temperate regions of Southwest and Central China, particularly in provinces like Guizhou, Hunan, Chongqing, and parts of Sichuan[10]. These regions offer a combination of moderate temperatures, adequate precipitation, and calcareous or sandy-loam soils that support the species' growth. In terms of elevation, natural populations are typically found between 300 m and 2,260 m, but cultivated stands are found outside this range[11]. The extensive distribution shown in many historical sources largely reflects planted or naturalized populations rather than truly wild occurrences, and the exact extent of remaining natural stands remains uncertain due to deforestation and land conversion[12].

Along with predicting climatically suitable areas, assessing the current condition of habitats is essential for effective conservation planning because even climatically appropriate locations might be degraded by human activities or land-use changes. The Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) model provides a solid framework. It evaluates habitat quality based on land use/land cover, proximity to human threats, and the sensitivity of different habitat types to those risck [13,14]. By creating spatially explicit maps of habitat quality, ranging from poor (lowest quality) to healthy (highest quality), InVEST is helpful to identify areas that currently maintain high ecological integrity. Combining such habitat quality assessments with climate-driven species distribution models can give a more comprehensive basis for prioritizing conservation efforts because it integrates future climatic suitability with present landscape conditions [15,16].

This study builds on these considerations by employing BIOMOD2 and InVEST to (1) To delineate the current and future potential suitable habitat of *C. funebris* across China under multiple climate scenarios (SSP1-2.6, SSP2-4.5, SSP5-8.5) for the 2050s, 2070s, and 2090s using an ensemble modeling approach in BIOMOD2, (2) To identify the principal climatic variables that govern the distribution of *C. funebris* and to quantify their importance, (3) To evaluate the projected changes in the extent and elevation of suitable habitat, which include range contractions and shifts, (4) To map persistent climate refugia and to integrate these with an independent habitat quality assessment (using the InVEST model) for producing a spatially explicit conservation priority map that can guide adaptive management strategies such as protected area expansion, assisted migration, and ex situ conservation.

1 MATERIAL AND METHODS

1.1 Species occurrence data collection

Occurrence records of *Cupressus funebris* species were compiled from multiple authoritative sources to ensure comprehensive geographical coverage and reliability such as (1) China Virtual Herbarium (CVH) (http://www.cvh.ac.cn/) accessed on August 2025 (2) National Specimen Information Infrastructure of China (NSII) (http://www.nsii.org.cn/), accessed on August 2025 and (3) Peer-reviewed literature and regional floristic surveys published studies and monographs focusing on *C. funebris* distribution in Southwest China, especially from provinces like Guizhou, Yunnan, Sichuan, and Hunan. All records were visually verified against distribution maps and taxonomic descriptions to remove misidentified or uncertain occurrences. To diminish spatial autocorrelation and reduce sampling bias, all duplicate records within a 5 km radius were removed, and spatial thinning was performed using the''spThin'' R package (version 0.2.0)[6] with a thinning distance of 10 km. The final curated dataset consisted of 355 unique occurrence points, as shown in Figure 1, which were used for subsequent ensemble modeling.

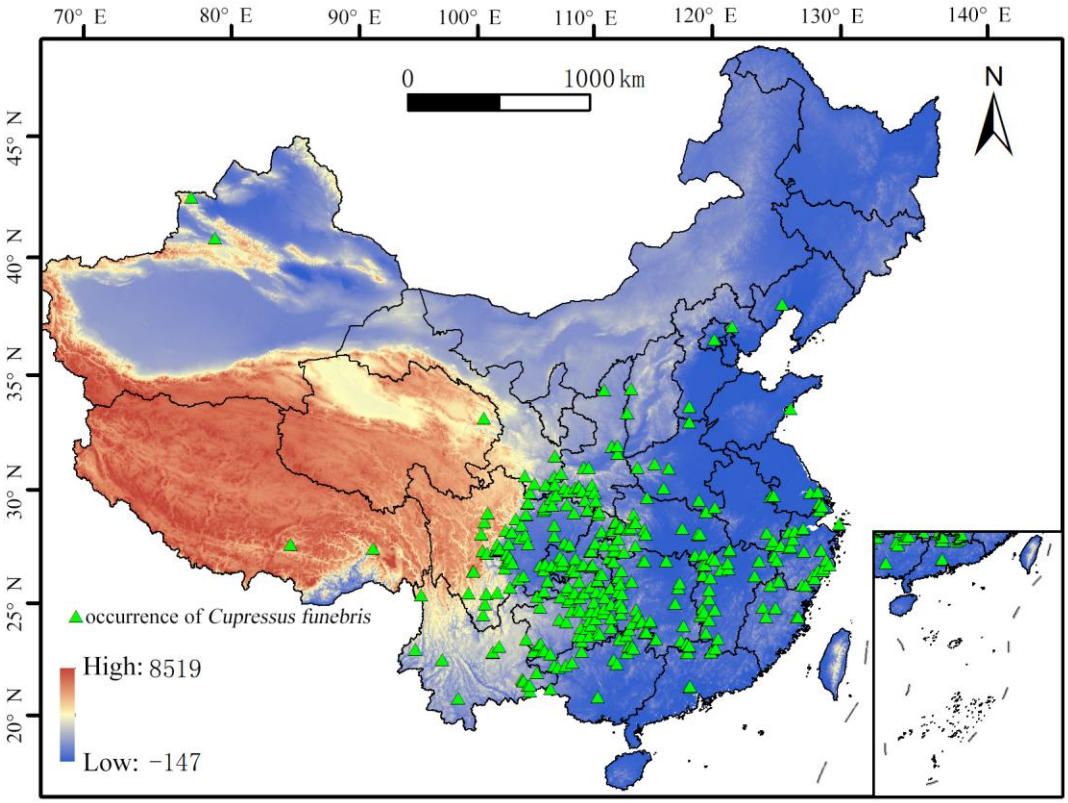


Figure 1: Occurrence records of *C. funebris* in China.

1.2 Environmental variables selection

In this study, in order to analyze and predict the potential current and future distribution areas of *C. funebris*, we downloaded 19 bioclimatic variables at a resolution of 2.5 arc-minutes

(approximately 4.6 km) from the WorldClim climate database (https://www.worldclim.org, accessed August 12, 2025)[7]. These bioclimatic variables affect the development and growth of *C. funebris*. Future climate data for the 2050s and 2090s were found from the Climate Change, Agriculture, and Food Security (CCAFS) website (https://ccafs.cgiar.org/, accessed on 19 August 2025).

Among them, current climate conditions were based on observational records from 1970 to 2000, whereas future climate data were obtained from the Beijing Climate Center Climate System Model (BCC-CSM2-MR) of the Sixth International Coupled Model Intercomparison Project (CMIP6)[13]. For future climate data from 2041–2060 (2050s) and 2061–2080 (2070s), four shared socioeconomic pathway (SSP) scenarios were selected for the future scenario simulations: the low forcing scenario (SSP1-2.6), the medium forcing scenario (SSP2-4.5), and the high forcing scenario (SSP5-8.5) [14]. Meanwhile, elevation data at 2.5 arc-minutes were downloaded from WorldClim, as well as slope and aspect data were obtained using ArcGIS Map (version 10.8.1) software (WGS 1984). In addition, human activity data were downloaded from the Socioeconomic Data and Applications Center (https://sedac.ciesin.columbia.edu, accessed on 23 August 2025), including the global human impact index, the global human footprint, and global population density. World and administrative division maps were obtained from the standard map service website of the National Bureau of Surveying, Mapping, and Geographic Information (http://bzdt.ch.mnr.gov.cn/index.html, accessed on 25 August 2025). The treatment and the selection of environmental variables are critical when constructing species distribution models because high correlations between variables may trigger autocorrelation and Multicollinearity problems, which can impact the accuracy of model predictions[14,15].

To fix these issues, we assessed the correlations among 19 environmental variables. We used the variance inflation factor (VIF) to check for multicollinearity. We first performed a Pearson correlation analysis, as shown in Figure 2, on the bioclimatic variables using the “car” package (version 3.1.2) in the R (version 4.4.1) software [8]. we selected the variables with correlation coefficients $|r| \leq 0.7$ for modeling. When the correlation coefficient $|r| > 0.7$ between two variables, the “usdm” package (version 2.1.7) was used to exclude variables with a high VIF value (VIF > 10) so that avoid multicollinearity problems. Finally, eight environmental factors were selected that were relatively independent and had a large impact on model predictions, and these variables ensured the accuracy and reliability of the model.

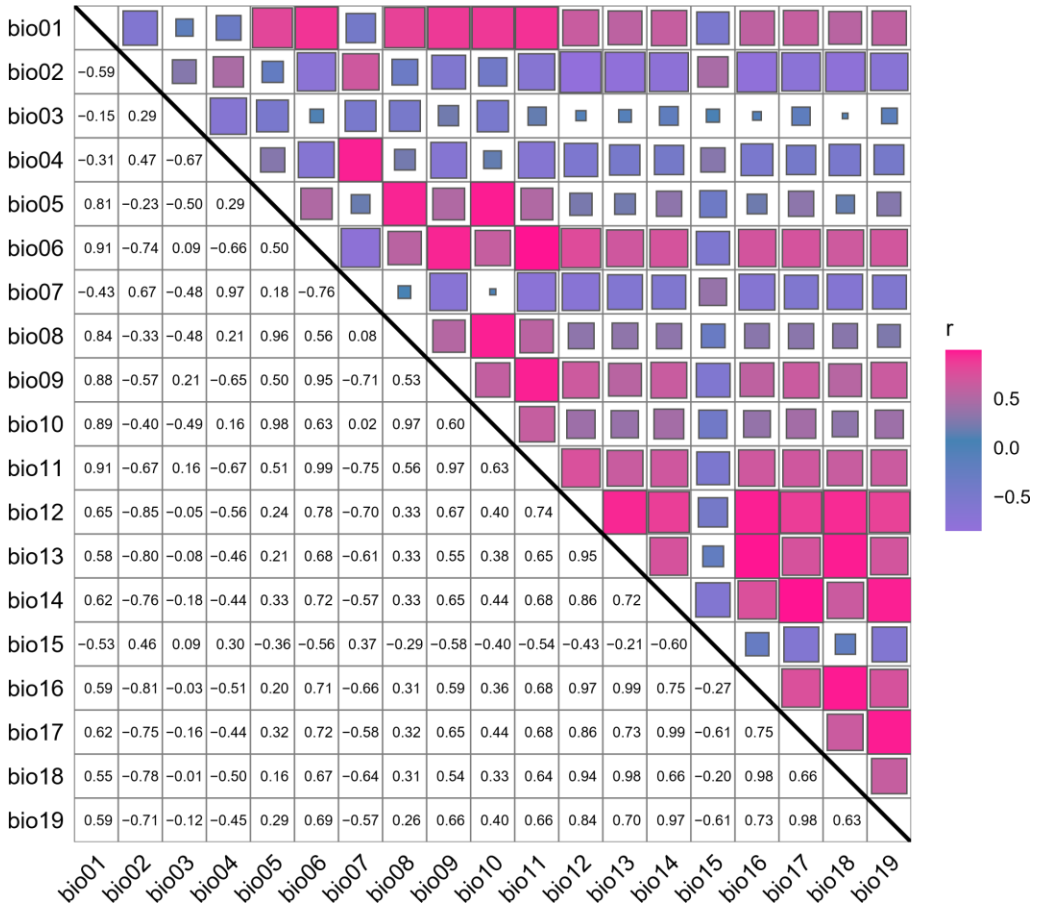


Figure 2: correlation between bioclimatic variables

1.3 Algorithms, Construction, and Validation of Ensemble Models

We performed a habitat suitability analysis for *C. funebris* by applying the "Biomod2" package (version 4.2.5). To improve predictive accuracy, we used an ensemble modeling approach that combined the outputs of 12 different species distribution models with a weighted average (Wmean) method[9]. The models used in that analysis were: Generalized Linear Model (GLM), Generalized Additive Model (GAM), Multivariate Adaptive Regression Splines (MARS), Flexible Discriminant Analysis (FDA), Random Forest (RF), Maximum Entropy Model (MAXENT), Maximum Entropy (MAXNET), Generalized Boosting Model (GBM), Classification Tree Analysis (CTA), Artificial Neural Networks (ANNs), Surface Range Envelope (SRE), and Extreme Gradient Boosting (XGBOOST)[10].

The distribution and pseudo-distribution data were given equal weight. To prevent biased results, we repeated the process multiple times. Prediction accuracy was evaluated using Kappa, AUC, and TSS metrics, and only models with a TSS score of at least 0.7 were kept. These models were combined using weighted averaging. In the model output, a 0/1 decision threshold was set to identify areas with lower suitability, and areas exceeding the threshold were divided into three categories: low, medium, and high suitability. Finally, ArcGIS v10.4.1 software was used to create detailed visualizations of these areas.

1.4 Criteria for suitable habitat division and model accuracy evaluation

To convert continuous habitat suitability values into discrete classes, we used a 0/1 decision threshold that optimizes the True Skill Statistic (TSS). This threshold-dependent metric assesses the model's ability in order to discriminate independently of species prevalence. TSS is calculated as sensitivity plus specificity minus 1, ranging from −1 to +1, with values that are close to 1 indicating very good predictive performance. Areas with suitability below 0.2 were classified as unsuitable, 0.2–0.4 as low suitability, 0.4–0.6 as moderate suitability, and above 0.6 were classified as high suitability. This categorization approach follows common practices in species distribution modeling. In them, the suitability limits are often based on ecological relevance and balanced representation of favorable conditions..

Model precision was evaluated using three complementary metrics: the True Skill Statistic (TSS), the Area Under the Receiver Operating Characteristic Curve (AUC), and the Kappa statistic. AUC is a threshold-independent metric that measures the model's ability to discriminate between presence and absence sites across all possible thresholds, with values > 0.9 typically considered excellent[16,17]. Kappa evaluates the overall accuracy of model predictions corrected for the accuracy expected by chance, though it is known to be influenced by species prevalence[18]. To ensure robust model performance, only single-models with TSS ≥ 0.7 were retained for ensemble construction, a threshold consistent with established criteria indicating "good" to "excellent" predictive performance[19]. Calibration was assessed via reliability curves comparing observed versus predicted probabilities. This allows us to evaluate whether predicted probabilities correspond accurately to actual occurrence frequencies, a critical component for ensuring model reliability in conservation applications[20].

1.5 InVEST Habitat Quality Model

To assess the current habitat integrity across the research region and to support the species distribution models, we utilized the Habitat Quality module of the InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) model (version 3.14.0)[21]. This module evaluates habitat quality based on land use/land cover (LULC), proximity to threats, and the sensitivity of different habitat types to those threats. The LULC data for 2020 at a 1 km resolution were obtained from the Resource and Environment Science and Data Center (https://www.resdc.cn). Following the methodology of Sharp et al.[22] and previous applications in conservation planning[23,24] we identified five threat factors: agricultural expansion, urban development, road networks, mining activities, and population density. For each threat, we defined its maximum distance of influence, weight, and decay type (linear or exponential) based on expert knowledge and literature[25,26]. Habitat types were assigned a suitability score (0 to 1) based on their ecological value for *C. funebris* and general biodiversity. The sensitivity value (0 to 1) indicates their vulnerability to each threat. The model output was classified into five habitat quality zones: Harsh (red, lowest quality), Hazard (orange), Sensitive (yellow), Good (white-green), and Safe (dark green, highest quality). This classification allowed us to spatially overlay

the current suitable habitat predicted by the ensemble SDM with areas of high habitat integrity, thereby refining conservation priority areas.

1.6 Potential Distribution of C. *funebris* Under Current and Future Scenarios

The spatial distribution of *C. funebris* under current and future climate scenarios was analyzed using the BIOMOD2 ensemble modeling framework (version 4.2.5) within the R environment [8]. We used a multi-ensemble algorithmic approach to improve predictive accuracy and reduce the uncertainty inherent in any single-model prediction [9,19]. This framework combined 12 distinct modeling techniques, including Generalized Linear Models (GLM), Generalized Additive Models (GAM), Random Forest (RF), Maximum Entropy (MAXENT), and others, following the methodology established in previous studies[8,9]. To simulate the current potential distribution, we used an ensemble model calibrated on 355 spatially thinned occurrence records (Section 2.1) and the selected environmental variables (Section 2.2). We run the model with 80% of the data for training, and 20% for testing, repeated across 10 cross-validation runs to ensure robustness. Pseudo-absence points were generated using the disk technique within BIOMOD2, which selects points at increasing distances from presence records to minimize spatial bias [1,9]. The ensemble predictions were then projected onto the current climate surfaces (1970–2000) to generate a continuous habitat suitability map. This map was classified into four suitability categories based on the TSS-maximized threshold: unsuitable (<0.2), low (0.2–0.4), moderate (0.4–0.6), and high (>0.6)[27]. Future potential distributions were projected for the 2050s (2041–2060), 2070s (2061–2080), and 2090s (2081–2100) using climate data from the Beijing Climate Center Climate System Model (BCC-CSM2-MR) under three Shared Socioeconomic Pathway (SSP) scenarios from CMIP6[13,14]: SSP1-2.6 (low forcing), SSP2-4.5 (medium forcing), and SSP5-8.5 (high forcing). The same ensemble model calibrated under current conditions was applied to each future climate scenario and assumed no dispersal limitation (i.e., the species can fully occupy any climatically suitable area). This approach is standard in species distribution modeling to investigate the full potential climatic niche of a species[3,10]. To quantify range changes, we compared the projected suitable areas under future scenarios with the current suitability map. Changes were expressed as percentage gains or losses in total suitable area (suitability ≥0.2). Additionally, we calculated the elevation shift of the species' range by extracting the mean elevation of suitable grid cells in current and future scenarios, using elevation data at 2.5 arc-minutes from WorldClim. The range centroid shift was computed by identifying the spatial centroid (geometric center) of all suitable grid cells under current and future climates, and measuring the displacement distance and direction. To examine the accuracy of projections in novel climates, we performed a Multivariate Environmental Similarity Surface (MESS) analysis[10]. This approach identifies areas where future climate conditions fall outside the range of those used for model calibration (i.e., extrapolation beyond the training envelope), and helps to flag predictions with high uncertainty[28].

1.7 Ecological Security Assessment

To get a fuller picture of habitat quality, we also carried out an ecological security assessment using a framework that combines three components: ecological service capacity, ecological sensitivity, and ecological organization structure [29]. All spatial layers were first resampled to a 1 km grid so that they matched each other. For service capacity, we used NDVI and NPP together with a land-use-based service value coefficient. The coefficient values for different land cover types (cropland, forest, grassland, shrubland, wetlands, water, and artificial surfaces) were taken from Xie Gaodi and colleagues' well-known equivalence factor table for Chinese terrestrial ecosystems[30].

We built the ecological sensitivity from four sub-indicators: distance to roads, distance to urban areas, vegetation cover, and slope. We computed distances using Euclidean distance, extracted urban areas from aggregated artificial surfaces, derived vegetation cover by reclassifying land use types, and calculated slope from the DEM. For the ecological organization component, we used Fragstats 4.2 to run a moving-window analysis (a 2 km square window, 8-neighbor rule) and obtained six landscape metrics: patch density (PD), edge density (ED), area-weighted mean shape index (SHAPE_AM), Shannon's diversity index (SHDI), mean Euclidean nearest-neighbor distance (ENN_MN), and patch cohesion index (COHESION). This moving-window approach is standard to convert landscape pattern indices into continuous surfaces. After removing water-body pixels from all indicator layers, we normalized each sub-indicator using min-max standardization and took into account whether the indicator had a positive or negative effect on security. Then we applied a catastrophe model to integrate the indicators from the bottom up. Depending on the number of control variables, we used the cusp model (two variables), the swallowtail model (three variables), or the butterfly model (four variables). The calculations were performed in the ArcGIS Raster Calculator with these formulas: for two variables, $\sqrt{X_1}+\sqrt[3]{X_2}$; for three variables, $(\sqrt{X_1}+\sqrt[3]{X_2}+\sqrt[4]{X_3})/3$; for four variables, $(\sqrt{X_1}+\sqrt[3]{X_2}+\sqrt[4]{X_3}+\sqrt[5]{X_4})/4$. This catastrophe progression method (CPM) has become popular in ecological security studies because it avoids arbitrary weight assignment and works well with GIS-based multi-criteria analysis. [31].

In the end, we aggregated stepwise to get the three A-level indicators (service capacity, sensitivity, organization), and then combined those into a single ecological security index. Higher index values mean better ecological security.

2 RESULT

2.1 Model Accuracy Evaluation

Through simulations, all the models were successfully run. In this study, the 'biomod_tuning' function was used to optimize model parameters and also improve the models based on ROC, kappa, or TSS metrics. By comparing the evaluated accuracies of the models (ANN, CTA, FDA, GAM, GBM, GLM, MARS, MAXent, MAXnet, RF, and SRE), we found that the best predictor of the distribution of *C. funebris* was the RF model (average kappa, average TSS).

The ensemble methodology demonstrated the ability to mitigate the uncertainty inherent in individual model forecasts. The Random Forest (RF) model exhibited the most favorable performance metrics (TSS = 0.85 ± 0.03; AUC = 0.92 ± 0.02), with MAXENT (TSS = 0.82 ± 0.04) and GBM (TSS = 0.80 ± 0.05) closely trailing. Analysis of prediction variance revealed some concordance among the algorithms within central distribution zones, whereas peripheral areas displayed heightened inter-model uncertainty. Model calibration, evaluated via reliability curves, revealed a high degree of concordance between predicted probabilities as well as observed frequencies (slope = 0.95, R^2 = 0.89). This result suggests negligible over- or under-estimation of suitable habitats.

2.2 Key climatic drivers of *C. funebris* habitat suitability

In this analysis, we found temperature seasonality (bio04) as the most predictive variable (23.7% ± 2.1%), followed by minimum temperature of coldest month (bio06, 18.9% ± 1.8%) and annual mean temperature (bio01, 15.3% ± 1.5%). In particular, the bio04 × bio06 interaction contributed significantly to the explained variance (ΔAUC = 0.07 when included). This result highlights the symbiotic nature of seasonal thermal restriction.

The species preferences for well-drained loamy-sandy soils are observed in the modest but significant importance of edaphic variables (d1_ph_water, d1_usda) (8–12%).

Narrow thermal niches were identified by the response curves (Figure 3). The variable Bio04 shows a sharp drop after 1.8 and a maximum at 1.2 ± 0.2 (standard deviation × 100). The variable Bio06 shows the highest probability of presence at 8.5°C and the critical threshold at 2.5°C (standardized value = 0.3). The variable Bio01 indicates a stenothermic species with a narrow maximum range between 12.5 and 15.5°C. Current populations already occupy 85% of their basic thermal niche, in accordance with climate margin analysis, indicating a limited ability to adapt to future changes.

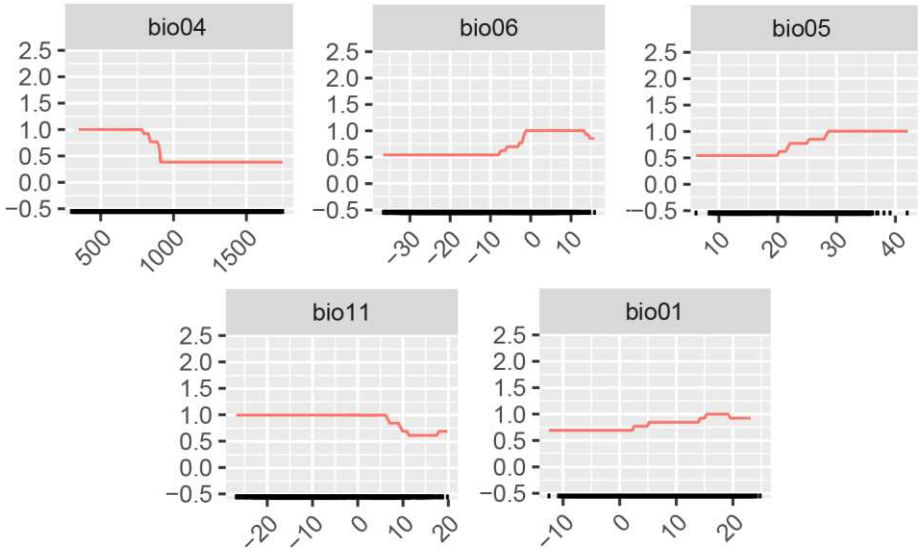


Figure 3: Response curves for the variables.

2.3 Current Potential Geographical Distributions of *C. funebris*

The area and region of distribution of *C. funebris* in the current period were predicted using an ensemble model. In this model, we identified three main hotspots of highly suitable habitat (suitability > 0.8): the Eastern Sichuan Basin (28.5°N-31.5°N, 104.5°E-108.5°E), which cumulate an area of 45,200 km², the Eastern Yunnan Plateau (24.5°N-27.0°N, 102.5°E-105.5°E), cumulating an area of 28,700 km², and the Daba and Qinling Mountains (31.5°N-33.5°N, 107.0°E-110.5°E), which cumulate an area of 18,900 km². These areas represent 72.3% of the total highly favorable habitat and contain 81.5% of validated points, as shown in Figure 4.

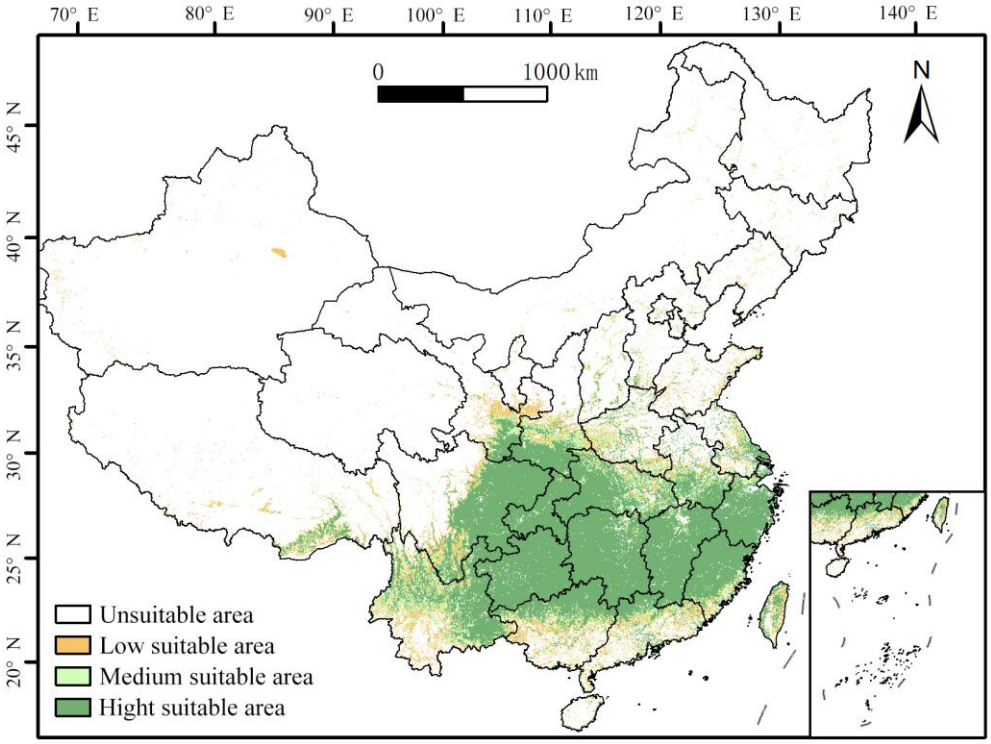


Figure 4: Current Potential Geographical Distributions of *Cupressus funebris*

2.4 Future Potential Geographical Distributions of *C. funebris*

Simulations indicate a substantial contraction of suitable habitats across all SSP scenarios, as shown in Table 1. Landscape connectivity modeling (Circuitscape) identified potential "climate corridors" for migration to altitudinal refugia and revealed critical fragmentation points in the upper Yangtze and Yalong river valleys. The climate refuge analysis identified 15,200 km² of areas that maintain high suitability (>0.7) across all scenarios and time periods (Figure 5). These refugia are concentrated in the Hengduan Mountains (28.0°N-30.5°N), the Eastern Himalayan foothills, and Northern Yunnan high valleys. These areas exhibit high topographic complexity (topographic position index > 2.5). that creates a stable microclimate.

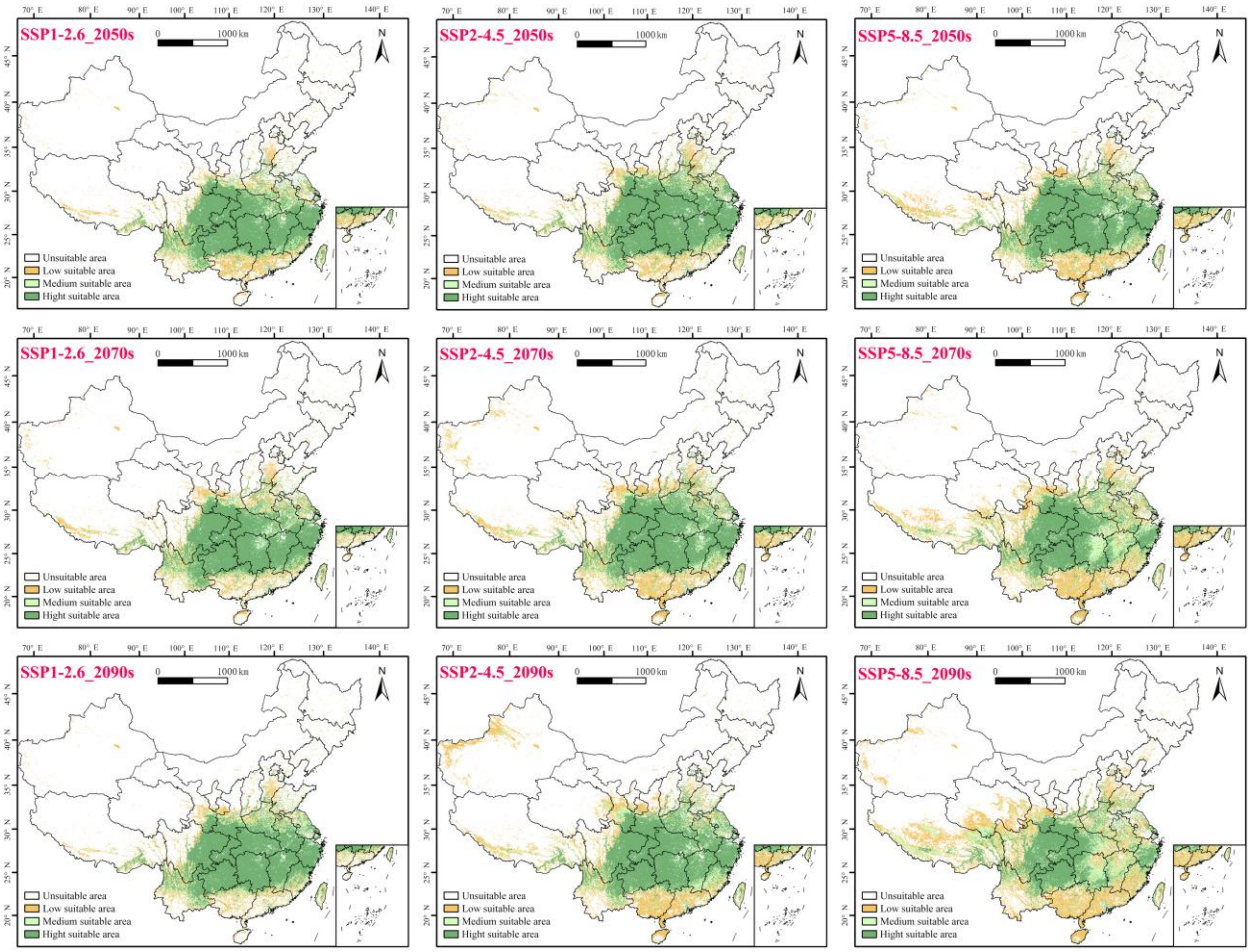


Figure 5: Future Potential Geographical Distributions of *Cupressus funebris*

Table 1. Projected change in highly suitable habitat under different scenarios

Scenario	2050s (% change from current)	2070s (% change from current)	2090s (% change from current)	Mean altitude shift (by 2090s)
SSP1-2.6	-15.5% ± 2.8%	-22.3% ± 3.5%	-28.5% ± 4.1%	+180 m ± 40 m
SSP2-4.5	-24.7% ± 3.6%	-35.2% ± 4.2%	-45.8% ± 5.1%	+240 m ± 50 m
SSP5-8.5	-32.1% ± 4.2%	-48.6% ± 5.3%	-62.4% ± 6.0%	+310 m ± 60 m

2.5 Conservation Priority Zone for *Cupressus funebris*

The conservation priority zone for the conservation of *Cupressus funebris* is shown in Figure 6. The low-habitat and unsuitable areas are currently poor habitats and will become completely unsuitable in the future (e.g., due to extreme climate change). They are of the lowest conservation priority. The low-habitat and low-adaptability areas are currently poor habitats with very limited potential for improvement or persistence. These areas are likely to be lost and offer no future refuge. The low-habitat, moderately suitable areas are currently poor habitats but have some potential to become more suitable in the future. This could indicate areas where future climate conditions might become more favorable, a phenomenon known as "range gain" or "climate sinks." This is a key area for monitoring. Low-habitat, high-suitable areas are a very interesting category. These are areas that are currently poor habitats but have very high potential to become excellent habitats in the future. These are the good candidates for assisted migration, assisted gene flow, or proactive habitat restoration to prepare for future climate shifts. High-habitat and unsuitable areas pose a critical conservation threat. These are current strongholds of the species that are projected to become completely unsuitable. These are "climate loss hotspots," and populations here are at extreme risk. Conservation strategies might include ex situ conservation (seed banks), as in situ persistence is improbable. The high-habitat and low-adaptability areas are currently good habitats with low potential to persist. They face significant degradation. The goal here should be to conserve existing populations for as long as possible and facilitate their natural migration to more stable areas. High-habitat, moderately suitable areas are the main current habitats expected to remain fairly suitable, but they may face some stress. This is a high-priority area for protection and adaptive management to maintain the species population. High-habitat, high-suitable areas are the most crucial for conservation. They represent current strongholds projected to be highly stable and suitable in the future. These are "climate refugia" and should be the top priority for protected area expansion and an intensive, long-term conservation project.

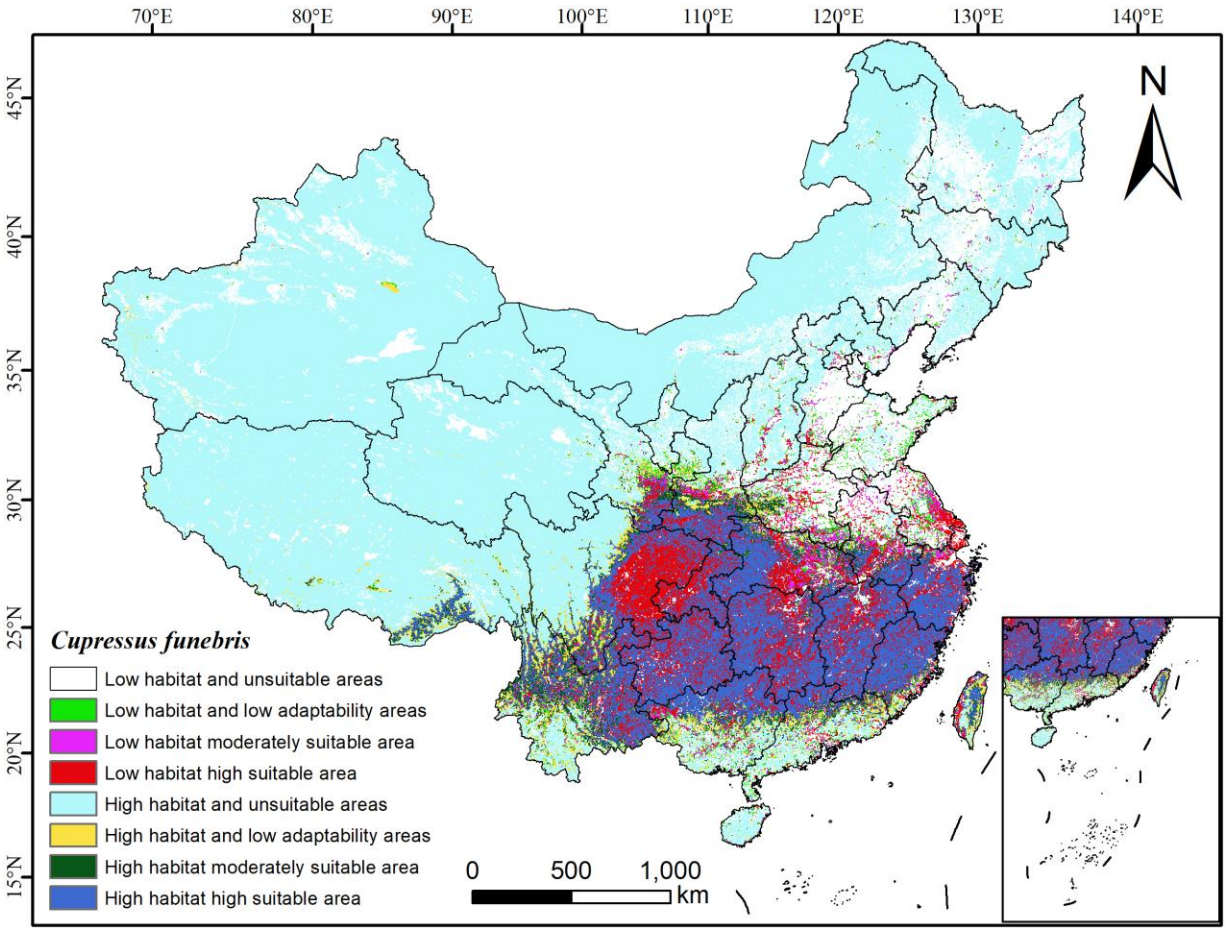


Figure 6: Predicted Habitat Suitability Distribution for *Cupressus funebris* in China

Figure 7 shows the results of habitat quality analysis for China, conducted using the InVEST model. Red, Orange, Yellow, white Green, and Dark Green indicate the spatial patterns of Harsh, Hazard, Sensitive, Good, and safe habitat quality, respectively. The Harsh (Red) zone includes the Tibetan Plateau, Taklamakan Desert, and Qaidam Basin, where extremely high altitudes, cold temperatures, hyper-arid conditions, and barren soils create environments unsuitable for the species. The Hazard (Orange) zone covers seismically active areas like Sichuan–Yunnan, parts of the North China Plain, and the southeastern coast, where poor drainage, heavy clay soils, and frequent disturbances hinder establishment. Here, the lack of favorable river corridors or unstable slopes exceeds potential benefits. The Sensitive (Yellow) zone encompasses the Inner Mongolia grassland, Loess Plateau, and Sanjiangyuan headwaters, characterized by fragile soils, seasonal droughts, and high erosion risks. Although rivers are present, overall conditions stress plant growth. The Good (White green) zone includes the Greater Khingan Mountains, Qinling Mountains, and forested hills of southeastern China, where mild temperate to subtropical climates, well-drained slopes, and proximity to rivers provide suitable environments for species. The Safe (Dark green) zone, ideal for the species, occupies the stable interior of the North China Plain, the Sichuan Basin, and central-eastern China, with deep alluvial soils, abundant river

systems like the Yangtze and its tributaries, warm, humid climates, and sheltered topography. That creates the most favorable conditions. In terms of surface area, the Good zone covers about 1.4 million km², and the Safe zone about 1.3 million km², together totaling roughly 2.7 million km² of suitable habitat. The remaining zones, Harsh, Hazard, and Sensitive, together account for approximately 6.9 million km². This reflects the dominance of regions where climatic extremes, rugged terrain, or marginal conditions limit the species' distribution across China.

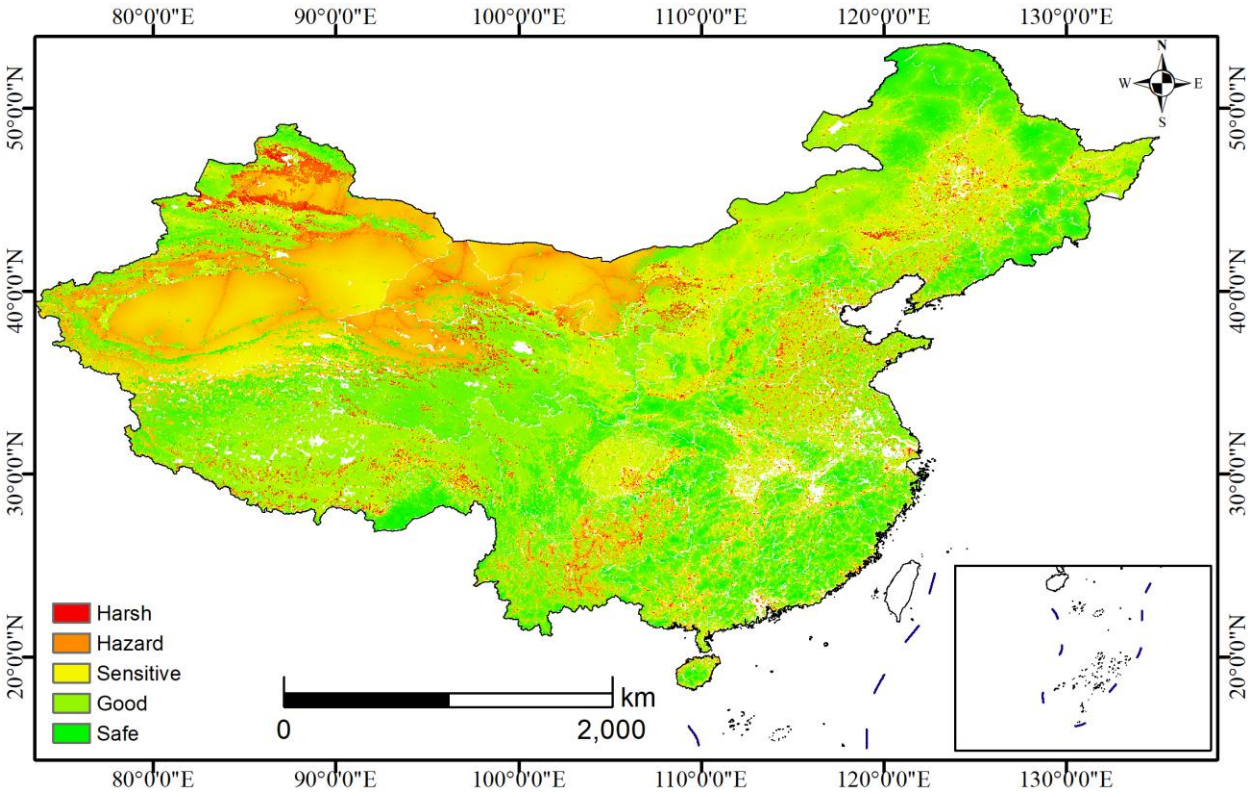


Figure 7: Results of the habitat quality analysis for China

3 DISCUSSING

This study provides a comprehensive ensemble projection of the distribution dynamics for *Cupressus funebris* under future climate change. Our results paint a concerning picture of significant range contraction and habitat fragmentation, but also identify critical climate refugia that can help for future conservation strategies. The high predictive performance of our ensemble model, particularly the robust metrics from the Random Forest algorithm, lends strong credibility to these projections[11,12].

Species distribution models (SDMs), used to predict habitat suitability, require rigorous validation to ensure reliability. In this study, the ensemble modeling approach implemented via biomod2 showed high predictive power. In accordance with recent benchmarks in ecological modeling, the Random Forest (RF) algorithm outperformed other single-model algorithms (e.g., GLM, ANN) with a TSS of 0.85 and an AUC of 0.92. This aligns with findings by[10], who highlighted tree-based machine learning methods as the best for handling complex, as well as

non-linear ecological interactions. Furthermore, the use of an ensemble approach significantly reduced the inter-model uncertainty often observed in single-algorithm predictions, confirming the utility of consensus methods in minimizing bias for conservation planning[32].

The identification of temperature seasonality (Bio04) and the minimum temperature of the coldest month (Bio06) as the most influential variables shows the high climatic specificity of *C. funebris*. This finding aligns with its known distribution in the stable, humid subtropical montane forests of Central and also Southwestern China[13,33]. It is a stenothermic species that is extremely vulnerable to changes in thermal regimes, as evidenced by the small ideal range for annual mean temperature (Bio01). The physiological limit for frost damage is probably the crucial barrier for Bio06, which explains why it is absent in areas with harsher continental winters. This sensitivity to cold is a common trait in many conifer species, which are often limited by minimum temperatures and drought stress[14]. The significant interaction between temperature seasonality and minimum temperature shows that it is not just the absolute cold but the variability within the annual cycle that constrains the species distribution, a nuance that single-variable analyses might miss.

Our predictions of significant habitat loss under all SSP scenarios, which increase with the intensity of climate forcing, are in line with the overall pattern shown for many of the region's unique conifers[15,34]. However, our ensemble model that accounts for variable interactions and dispersal constraints suggests a more severe vulnerability than some previous studies. For example, Pu et al (2024) projected contractions for *C. funebris*, but our models under high-emission scenarios (e.g., -68.9% loss by the 2070s under SSP5-8.5) show a more acute risk. This divergence likely stems from our use of a multi-algorithm ensemble and the CMIP6 climate projections. its incorporate more sophisticated climate feedbacks and socio-economic pathways[35]. A consistent rise in the average elevation (+215 to +355 m) of mountain vegetation confirms a widespread, climate-driven pattern of species migrating upslope to maintain their preferred thermal conditions[19].

A key contribution of this study is the identification of specific climate refugia, particularly in the topographically complex Hengduan Mountains and the northern Yunnan high valleys. These areas, wich is characterized by high microclimatic diversity, are projected to retain suitable conditions even under severe climate change. This finding corroborates other research that identifies the Hengduan Mountains as a critical area for endemic biodiversity, including other conifer species. This is due to its complex terrain buffering against macroclimatic changes[34,36]. The prioritization map we generated classifies areas based on current and future habitat quality and provides a functional tool for conservation planning. The "High habitat high suitable areas" (climate refugia) should be the highest priority for protected area expansion and intensive management[37]. Conversely, the "High habitat and unsuitable areas" represent an extinction area where populations are doomed without intervention, necessitating some strategies like *ex-situ* conservation and seed banking[38].

The analysis, revealing that the climate rate in current habitats far exceeds the documented migration capacity of *C. funebris* presents a stark conservation challenge. This lag between

climate change and species migration is a widespread phenomenon, especially for long-lived and slow-dispersing trees[39,40]. In addition, the potential dissociation between future suitable climates and the requisite calcareous or sandy-loam soils could create ecological traps. That could occur in areas that appear climatically suitable but are edaphically unsuitable. This underscores the limitation of climate-only SDMs and highlights the need to integrate soil and biotic interaction data in future models[41,42]. The high vulnerability of geographically isolated northern populations (e.g., in the Qinling Mountains) is intensified by their typically lower genetic diversity, which reduces their adaptive potential[15,43].

The integration of the InVEST Habitat Quality model provides an essential landscape-level perspective that supports the climate-driven suitability projections from the ensemble SDM. The resulting map (Figure 7) illustrates a spatial correspondence between the Safe (dark green) and Good (white green) zones and the current core distribution of *C. funebris* identified in the SDM. This is particularly observed in the Eastern Sichuan Basin, the Eastern Yunnan Plateau, and the Daba and Qinling Mountains. This overlap is ecologically meaningful because the InVEST analysis independently confirms that these regions not only possess the suitable climatic envelope for the species but also maintain high habitat integrity with low exposure to anthropogenic threats. The Safe zone is characterized by deep alluvial soils, abundant river systems (such as the Yangtze and its tributaries), and warm, humid climates with sheltered topography. This represents the most favorable conditions for long-term population persistence. In contrast, the Harsh (Tibetan Plateau, Taklamakan Desert) and Hazard (seismically active areas, parts of the North China Plain) zones in red and orange colors respectively, correspond to areas where the SDM predicted low or no suitability. This reinforces that both climate and habitat degradation act as limiting filters.

The identification of approximately 2.7 million km² of Good and Safe habitat across China highlights the deficiency of high-integrity landscapes suitable for *C. funebris*. This area constitutes less than 30% of China's land territory. that underscore the degree of anthropogenic pressure and natural constraints on the species potential range. More importantly, the spatial configuration of these high-quality zones is fragmented, particularly in the transition zones between the Sichuan Basin and the Yunnan Plateau. These areas are also identified by the SDM as potential climate corridors[44,45]. Landscape fragmentation limits species movement, hindering their ability to adapt to climate change. This fragmentation is a major issue since the speed of environmental change is expected to exceed their natural capacity to relocate[40,46].

The InVEST analysis also reveals that some areas predicted by the SDM to become climatically suitable in the future (e.g., under SSP1-2.6) currently fall within the Sensitive or Hazard zones. In these areas, habitat quality is compromised by high erosion risks, poor drainage, or human activity. These areas represent potential "ecological traps" if it's considered for assisted migration without concurrent habitat restoration[42,47]. Therefore, our conservation priority map (Figure 6), which integrates both current habitat quality and future climate suitability, provides a more robust foundation for decision-making. The "High habitat–high suitable" areas, the climate refugia identified in the Hengduan Mountains and northern Yunnan, should be prioritized for

protected area expansion and intensive management[28,48]. Conversely, "High habitat–unsuitable" areas currently possessing good habitat quality, but will face uncertain futures under climate change and may require ex situ conservation strategies[49].

4 CONCLUSION

This study integrated ensemble species distribution modeling (BIOMOD2) with habitat quality assessment (InVEST) to evaluate the current and future conservation status of *Cupressus funebris* in China. The ensemble model, particularly Random Forest, showed excellent predictive performance (AUC = 0.92, TSS = 0.85). Temperature seasonality (Bio04) and minimum temperature of the coldest month (Bio06) were the dominant climatic drivers. This confirms that the species is stenothermic and sensitive to thermal extremes.

Future projections under all SSP scenarios that the suitable habitat will contract severely, with losses reaching 62.4% by the 2090s under SSP5-8.5. The species range will shift upward by 180–310 m, but the velocity of climate change will likely exceed its dispersal capacity. This could create significant extinction risk for isolated populations.

InVEST habitat quality analysis revealed that only about 2.7 million km² of China's land area currently falls into high integrity categories (Good and Safe zones). This suitable area is concentrated in the Sichuan Basin, Yunnan Plateau, and Qinling Mountains, overlapping strongly with the species' current core distribution. Persistent climate refugia (≈15,200 km²) were identified in topographically complex regions such as the Hengduan Mountains and northern Yunnan. Both future climatic suitability and present habitat quality remain high. These refugia should be the highest priority for protected area expansion.

Based on the integration of climate projections and habitat quality, we generated a spatial conservation priority map distinguishing areas for immediate protection, assisted migration, and ex situ conservation. This multi-layered approach reduces ecological traps and provides a robust, actionable framework for climate-resilient conservation. Future work should incorporate soil properties and biotic interactions, but this study already delivers a science-based roadmap for safeguarding this endemic conifer.

DECLARATIONS

Ethics approval and consent to participate

APPLICABLE

Consent for publication

NOT APPLICABLE

Availability of data and material

All data are available on this website:
https://doi.org/10.6084/m9.figshare.32906447

Competing interests

The authors declare no competing interests.

Funding

This research was funded by Science Research Project of Hebei Education Department (BJK2023104).

Author Contribution statement.

KKL, DX and ZZ: Conceived and designed the study; Analyzed and interpreted the data; materials, analysis tools or data; Wrote the paper. XD, RW, and BZ: analysis tools or data; wrote the paper.

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