

## Article

# Climatic Suitability of *Cornus officinalis* Across Paleoclimatic, Current, and Future Climates: Implications for Conservation and Climate-Informed Cultivation

Yongxiang Li <sup>1,†</sup> , Tingyao Zhang <sup>1,2,†</sup>, Haoyu Zhou <sup>1,2</sup>, Bin Wang <sup>3</sup>, Peilin Xu <sup>1</sup>, Honggang Sun <sup>1</sup>, Fucai Xia <sup>2</sup> and Wenhao Shao <sup>1,\*</sup> 

<sup>1</sup> Key Laboratory of National Forestry, Grassland Administration on Forest Cultivation, Management in East China, Research Institute of Subtropical Forestry, Chinese Academy of Forestry, Hangzhou 311400, China

<sup>2</sup> College of Forestry, Beihua University, Jilin 132013, China

<sup>3</sup> Longshan Forest Farm, Anji County, Huzhou 313306, China

\* Correspondence: whshao8119@163.com

† These authors contributed equally to this work.

## Highlights

### What are the main findings?

- An optimized MaxEnt model identified cold-quarter temperature and warm-season precipitation as the dominant climatic factors shaping the suitability of *Cornus officinalis*.
- Future projections showed net losses and northward redistribution of climatically suitable areas under all SSP scenarios, with the strongest decline in highly suitable areas under SSP3-7.0 and SSP5-8.5.

### What are the implications of the main findings?

- Climatically stable areas can support priority setting for germplasm conservation, long-term monitoring, and climate-informed cultivation planning.
- Newly suitable areas supported by multiple GCMs provide candidate regions for field evaluation and experimental introduction rather than definitive cultivation zones.

## Abstract

*Cornus officinalis* Sieb. et Zucc. is a medicinal and ornamental woody plant whose distribution and production may be increasingly affected by climate change. This study assessed its climatic suitability under paleoclimatic, current, and future conditions to provide a climatic basis for cultivation planning, introduction, and germplasm conservation. An optimized MaxEnt model was developed using 381 spatially filtered occurrence records and five environmental predictors. Model complexity was tuned using spatial block cross-validation, and future projections for 2081–2100 were generated from an ensemble of ACCESS-CM2, BCC-CSM2-MR, and CMCC-ESM2 under four Shared Socioeconomic Pathway scenarios. Cold-quarter temperature, warm-season precipitation, mean diurnal temperature range, precipitation seasonality, and slope jointly shaped the predicted distribution. Under the current climate, climatically suitable areas were concentrated mainly in East Asia, particularly central and eastern China, with additional suitable climatic regions in eastern North America and parts of Europe. Suitable area was smallest during the Last Interglacial, expanded during the Last Glacial Maximum, and approached its current extent during the Mid-Holocene. The current suitable area was estimated at  $277.247 \times 10^4 \text{ km}^2$  and was projected to decrease to 243.689, 206.615, 201.393, and  $206.168 \times 10^4 \text{ km}^2$  under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5, respectively. Existing suitable areas contracted in central China,



Received: 27 June 2026

Revised: 1 August 2026

Accepted: 7 August 2026

Published: 10 August 2026

**Copyright:** © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

the southern United States, and southern Japan, whereas climatic suitability expanded northward in parts of China, North America, Japan, and Europe. Suitable-area gains did not offset losses under any scenario, and retention of current suitable areas declined from 52.88% under SSP1-2.6 to 19.74% under SSP5-8.5. Most newly suitable areas were supported by at least two of the three climate models, although greater inter-model variation occurred near some range margins. These findings indicate substantial future redistribution of climatic suitability and identify climatically stable and newly suitable regions that may inform climate-resilient cultivation planning and conservation of *C. officinalis*.

**Keywords:** *Cornus officinalis*; climatic suitability; MaxEnt; species distribution modelling; climate change

## 1. Introduction

*Cornus officinalis* Sieb. et Zucc. (Cornaceae) is a deciduous woody species whose dried sarcocarp is widely used as the traditional Chinese medicine Shanzhuyu, or Corni Fructus. It is also an important medicinal and ornamental horticultural resource, valued for its bright yellow flowers in early spring, red fruits in autumn, and potential use in mountainous agroforestry, landscape planting, and ecological restoration systems. In traditional Chinese medicine, *C. officinalis* was recorded as a medium-grade medicinal material in *Shennong's Classic of Materia Medica* and has long been used to tonify the liver and kidney, astringe seminal discharge, and consolidate essence [1]. Modern pharmacological studies have shown that *C. officinalis* contains abundant bioactive compounds, including iridoid glycosides such as loganin and morroniside, flavonoids, polysaccharides, and triterpenoids, which are associated with antioxidant, anti-inflammatory, hypoglycemic, neuroprotective, and immunomodulatory activities [2,3]. These medicinal and horticultural values have increased interest in the conservation, introduction, and sustainable production of the species. Increasing market demand and the decline of wild resources have made artificial cultivation the main approach for ensuring a stable supply of *C. officinalis* medicinal materials. In China, commercial production is concentrated mainly in Henan, Shaanxi, and Zhejiang provinces, but introduction and cultivation have gradually expanded beyond these traditional production areas [2,4]. However, cultivation expansion without systematic ecological suitability assessment may result in unstable growth performance, inconsistent medicinal quality, and inefficient land use [5]. A clearer understanding of the climatic conditions associated with the species' distribution is therefore important for guiding regional cultivation planning, protecting existing production bases, and supporting the sustainable use of its germplasm resources.

Climate change is reshaping the environmental conditions that determine where horticultural crops and medicinal plants can be cultivated reliably. Continued warming, altered precipitation regimes, and more frequent extreme climatic events may affect phenology, overwintering survival, water availability, pest pressure, yield stability, and product quality [6–8]. These effects are particularly relevant for perennial woody medicinal plants such as *C. officinalis*, because orchard or production-base establishment requires long-term planning and substantial investment. Unlike annual crops, long-lived woody plants may remain exposed to changing climatic conditions for decades, making present-day planting decisions increasingly dependent on future climate trajectories [9,10]. Predicting climatically suitable areas under historical, current, and future climatic conditions can therefore provide useful information for climate adaptation, horticultural resource management, and the sustainable utilization of medicinal plant resources. Species distribution models (SDMs)

provide a practical framework for linking species occurrence records with environmental variables and have been increasingly used in crop suitability assessment, introduction risk evaluation, and climate-change adaptation studies [11–13]. Among these models, the maximum entropy algorithm, MaxEnt, has been widely applied because of its strong performance with presence-only data and relatively limited occurrence records [14]. By integrating occurrence records with climatic and topographic variables, MaxEnt can identify the main environmental constraints on climatic suitability and predict how suitable areas may shift under different climate scenarios [12,14]. When combined with model tuning, spatially structured evaluation, and multiple climate projections, this approach can provide a more robust assessment of both climatic suitability and projection variability.

Previous studies on *C. officinalis* have mainly focused on phytochemistry, quality evaluation, germplasm resources, and regional ecological suitability [15–18]. However, existing suitability assessments have often been limited by restricted occurrence coverage, regional study extents, reliance on a single model configuration or climate projection, or the inclusion of only a narrow range of climatic periods, leaving the long-term dynamics and future redistribution of climatically suitable areas insufficiently resolved. Moreover, uncertainty arising from the choice of future climate model has rarely been explicitly considered. To address these gaps, we integrated spatially filtered wild-occurrence and herbarium records with an optimized MaxEnt model and spatial analyses to identify the main environmental factors associated with the distribution of *C. officinalis*, reconstruct changes in climatic suitability from the Last Interglacial to the present, and project future redistribution under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 using an ensemble of three global climate models. Model complexity was optimized and evaluated using spatial block cross-validation, while inter-model agreement and variation were explicitly assessed to avoid dependence on a single future climate model. By distinguishing poorly, moderately, and highly suitable climatic areas and quantifying their persistence, loss, gain, and inter-model agreement, this study provides a temporally integrated assessment of climatic suitability and a climatic basis for cultivation planning, experimental introduction, and germplasm conservation.

## 2. Materials and Methods

### 2.1. Occurrence Data

Global occurrence records of *C. officinalis* spanning 1863–2024 were obtained from the Global Biodiversity Information Facility (GBIF Occurrence Download. Available online: <https://doi.org/10.15468/dl.dbqz6t>, accessed on 25 February 2025), the National Specimen Information Infrastructure of China (NSII; <https://www.nsii.org.cn/2017/home-en.php>, accessed on 26 February 2025), and the Chinese Virtual Herbarium (CVH; <https://www.cvh.ac.cn/>, accessed on 26 February 2025). These records were supplemented with information from the Flora of China and field survey data. During data cleaning, records explicitly identified as cultivated, introduced, naturalized, or of uncertain origin were excluded, and only records that could be verified as wild occurrences were retained. Duplicate records, records lacking complete geographic coordinates or locality information, and records with coordinates inconsistent with the reported locality or accepted native range were also removed, resulting in 887 initial records. To reduce local spatial clustering and duplicate sampling of the same climatic grid cell, coordinate filtering was conducted using the ENMTools package in R v4.4.3. A single record was kept per 2.5 arc-minute grid cell, leaving 381 occurrence points for the global model. ArcGIS 10.8 was used to map the global distribution of *C. officinalis* (Figure 1) [12,19,20]. The global administrative boundary base map was obtained from the Resource and Environmental Science Data Center, Chinese Academy of Sciences.

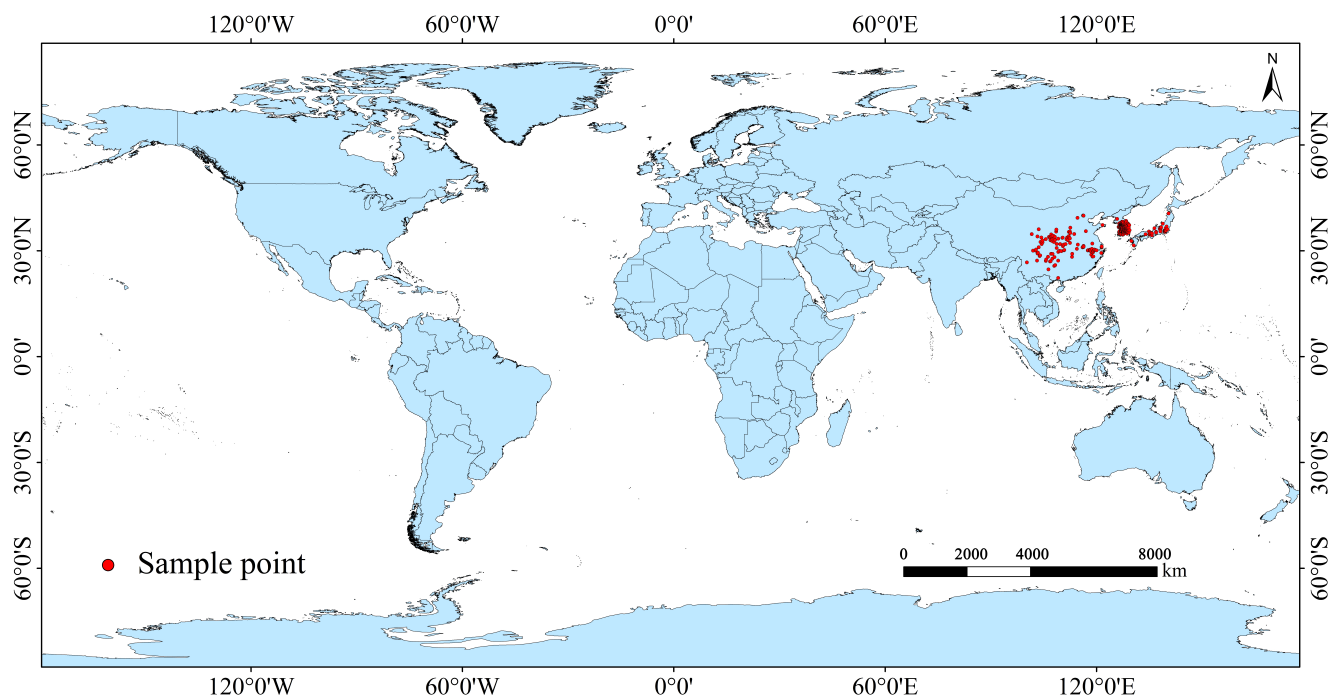


**Figure 1.** Global occurrence records used to model the climatic suitability of *C. officinalis*.

## 2.2. Environmental Variable Data

A total of 21 environmental variables were initially selected for MaxEnt modelling (Table 1), including 19 bioclimatic variables and two topographic variables. Current bioclimatic variables representing 1970–2000 were obtained from WorldClim v2.1. Paleoclimatic variables covered the Last Interglacial (LIG, ca. 120–140 ka BP), the Last Glacial Maximum (LGM, ca. 22 ka BP), and the Mid-Holocene (MH, ca. 6 ka BP). The LIG dataset was based on the simulations of Otto-Bliesner et al. [21] and included downscaled minimum temperature, maximum temperature, precipitation, and derived bioclimatic variables. The CCSM4 model was used for the LGM, whereas BCC-CSM1-1 was used for the Mid-Holocene. Future climatic variables represented 2081–2100 and were derived from CMIP6 under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. To account for variation among climate models, ACCESS-CM2, BCC-CSM2-MR, and CMCC-ESM2 were used [22–24].

**Table 1.** Environmental variables used for climatic suitability modeling of *C. officinalis*.

| Environment Variable | Description                                                | Unit |
|----------------------|------------------------------------------------------------|------|
| Bio1                 | Annual mean temperature                                    | °C   |
| Bio2                 | Mean diurnal range                                         | °C   |
| Bio3                 | Isothermality (Bio2/Bio7) ( $\times 100$ )                 | %    |
| Bio4                 | Temperature seasonality (standard deviation $\times 100$ ) | -    |
| Bio5                 | Max temperature of warmest month                           | °C   |
| Bio6                 | Min temperature of coldest month                           | °C   |
| Bio7                 | Temperature annual range (Bio5–Bio6)                       | °C   |
| Bio8                 | Mean temperature of wettest quarter                        | °C   |
| Bio9                 | Mean temperature of driest quarter                         | °C   |
| Bio10                | Mean temperature of warmest quarter                        | °C   |
| Bio11                | Mean temperature of coldest quarter                        | °C   |
| Bio12                | Annual precipitation                                       | mm   |
| Bio13                | Precipitation of wettest month                             | mm   |
| Bio14                | Precipitation of driest month                              | mm   |

Table 1. Cont.

| Environment Variable | Description                                          | Unit |
|----------------------|------------------------------------------------------|------|
| Bio15                | Precipitation seasonality (coefficient of variation) | -    |
| Bio16                | Precipitation of wettest quarter                     | mm   |
| Bio17                | Precipitation of driest quarter                      | mm   |
| Bio18                | Precipitation of warmest quarter                     | mm   |
| Bio19                | Precipitation of coldest quarter                     | mm   |
| Elevation            | Altitude                                             | m    |
| Slope                | Slope                                                | %    |

All climatic layers were converted to a common geographic coordinate system and aligned to a spatial resolution of 2.5 arc-minutes, approximately 5 km at the equator. Layers were resampled where necessary and matched to the same spatial extent, grid origin, number of rows and columns, and NoData definition. The global digital elevation model was obtained from NOAA-NCEI at a spatial resolution of 1 km, and slope was derived using the 3D Analyst tools in ArcGIS 10.8. The DEM and slope layers were resampled to the climatic grid using bilinear interpolation and aligned with the climatic rasters. All predictors were then clipped to the accessible calibration area for variable screening, background sampling, model tuning, and calibration, while aligned global layers were retained for broader spatial projection.

Future climatic suitability was projected separately for each GCM. For each SSP scenario, the pixel-wise mean of the three suitability rasters was used as the ensemble estimate. Pixel-wise standard deviation and the number of GCMs predicting each grid cell as suitable were also calculated to characterize inter-model variation and agreement.

### 2.3. Modeling and Spatial Analysis Methods

#### 2.3.1. Accessible Area Delimitation

To define the area accessible to *C. officinalis* for model calibration, a minimum convex polygon was constructed from the 381 spatially filtered occurrence records. The polygon was generated after transforming the occurrence data to an equal-area projected coordinate system and was subsequently expanded by a 1000 km buffer to delineate the accessible area (M). Defining an ecologically accessible calibration area is important because the selection of the background extent can influence model fitting, evaluation, and the inferred environmental niche [25]. The resulting polygon was transformed back to the geographic coordinate system and used to clip all environmental layers. Environmental-variable screening, background-point sampling, model tuning, and spatially structured model evaluation were conducted within this calibration area rather than across the global environmental extent.

#### 2.3.2. Environmental Variable Screening

An initial set of 21 environmental predictors, comprising 19 bioclimatic variables, elevation and slope, was considered. Aspect was excluded because of its circular nature and was not treated directly as a conventional continuous predictor. After the environmental layers were clipped to M, 100,000 raster cells with complete values for all 21 predictors were randomly sampled. Pairwise Pearson correlation coefficients were calculated, and predictor pairs with  $|r| \geq 0.80$  were considered highly correlated [26]. Multicollinearity was further evaluated using variance inflation factors. Variables were iteratively removed when the maximum VIF was  $\geq 10$ , with variables showing stronger overall correlations preferentially excluded. Ecological relevance and interpretability were also considered when selecting among correlated predictors. The final predictor set comprised mean diurnal temperature range (Bio2), mean temperature of the coldest quarter (Bio11), precipitation seasonality (Bio15), precipitation of the warmest quarter (Bio18), and slope (Table 2).

**Table 2.** Environmental predictors retained for MaxEnt modelling of *C. officinalis* after correlation and VIF screening.

| Variable | Predictor with the Highest  r | Pearson's r | Maximum  r | VIF   |
|----------|-------------------------------|-------------|------------|-------|
| Bio2     | Bio11                         | −0.651      | 0.651      | 2.784 |
| Bio11    | Bio2                          | −0.651      | 0.651      | 1.987 |
| Bio15    | Bio2                          | 0.625       | 0.625      | 1.735 |
| Bio18    | Bio11                         | 0.597       | 0.597      | 1.882 |
| Slope    | Bio18                         | 0.198       | 0.198      | 1.053 |

### 2.3.3. Model Parameter Optimization and Evaluation

Model complexity was optimized using ENMeval v2.0.5.2 in R with the maxnet algorithm [27]. Six feature-class combinations were evaluated, including linear (L), linear quadratic (LQ), hinge (H), linear quadratic hinge (LQH), linear quadratic hinge product (LQHP), and linear quadratic hinge product threshold (LQHPT). Regularization multipliers ranging from 0.5 to 4.0 at intervals of 0.5 were tested, resulting in 48 candidate parameter combinations. A total of 10,000 background points were randomly sampled within the accessible calibration area (M). Occurrence and background records were partitioned into four geographically structured folds using the spatial block method to reduce the influence of spatial autocorrelation and provide a more stringent assessment of model transferability [28,29]. Candidate models were assessed using validation AUC, the difference between training and validation AUC, the 10th-percentile omission rate (OR10), and the continuous Boyce index (CBI), which evaluates the consistency between predicted suitability and observed presences in presence-only models [30]. The optimal parameterization was selected by jointly considering discriminatory ability, omission error, spatial transferability, and model complexity rather than relying on a single evaluation metric. Based on this integrated assessment, the model combining linear, quadratic, hinge, and product features with a regularization multiplier of 0.5 was selected for final calibration and spatial projection.

### 2.3.4. Final Model Calibration and Current Projection

Following parameter optimization, the final model was fitted in MaxEnt v3.4.4 using the five retained predictors and the optimal parameterization identified by ENMeval [31]. Linear, quadratic, hinge, and product features were enabled, threshold features were disabled, and the regularization multiplier was set to 0.5. All 381 spatially filtered occurrence records were used for calibration, and duplicate presences within the same raster cell were removed automatically by MaxEnt. A maximum of 10,000 background points was sampled from the accessible calibration area (M) [25].

The final model was run once using the full occurrence dataset, with no replicate resampling or random test partition because model performance had already been evaluated using four-fold spatial block cross-validation. The random seed option was disabled to retain a fixed calibration dataset. Cloglog output was used to generate continuous climatic-suitability values ranging from 0 to 1 [31]. Response curves and Jackknife tests were produced to examine predictor–suitability relationships and the information contributed by individual environmental variables [32]. For descriptive interpretation of the single-variable response curves, predictor ranges associated with cloglog values of at least 0.5 were summarized as intervals of relatively high modeled suitability. This value was used only as a common reference for comparing response patterns and was not interpreted as an ecologically validated threshold, an absolute probability of occurrence, or the suitable–unsuitable cutoff used in spatial classification.

The model was calibrated using environmental layers restricted to M and subsequently transferred to aligned contemporary environmental layers covering the broader projection extent. Extrapolation and clamping were enabled during projection to constrain model responses under environmental conditions outside the calibration range, whereas fade-by-clamping was disabled. The resulting cloglog raster was used to characterize the current climatic suitability of *C. officinalis*.

Continuous predictions were classified using the 10th-percentile training presence threshold of the final model. This threshold allows a small proportion of calibration records to fall below the suitable–unsuitable boundary and may reduce sensitivity to positional uncertainty or atypical occurrence records. Because threshold choice can substantially affect the extent and interpretation of binary species-distribution predictions, the same cutoff was applied consistently across all projections [33]. The 10th-percentile training-presence cloglog threshold of 0.209 was used to distinguish suitable from unsuitable habitat, thereby allowing for a limited proportion of occurrence records potentially affected by positional error or marginal environmental conditions [33]. The remaining interval from 0.209 to 1 was divided into three equal-width classes: poorly suitable (0.209–<0.473), moderately suitable (0.473–<0.736), and highly suitable ( $\geq 0.736$ ). These thresholds were applied consistently to current, paleoclimatic, and future projections to ensure comparability among periods and scenarios.

#### 2.3.5. Future Climatic Suitability Projection and Multi-GCM Ensemble Analysis

The final MaxEnt model was projected onto future climatic conditions for 2081–2100 under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. Future bioclimatic variables were obtained from three CMIP6 global climate models (GCMs): ACCESS-CM2, BCC-CSM2-MR, and CMCC-ESM2 [34]. For each SSP scenario, projections were generated separately for the three GCMs using the same occurrence records, environmental predictors, model parameters, and cloglog output format as the current model. Extrapolation and clamping were retained during projection to constrain model responses under environmental conditions outside the calibration range. For each SSP scenario, the three continuous suitability rasters were combined by calculating their pixel-wise mean, which was used as the ensemble projection of future climatic suitability. Combining projections from multiple climate models reduces reliance on any single GCM and allows the shared spatial signal and inter-model variation to be evaluated [35,36]. Pixel-wise standard deviation was calculated to characterize variation in continuous suitability among the three GCMs. Each GCM projection was also converted into a binary suitable–unsuitable map using the threshold of 0.209. Binary maps were summed to produce an agreement index ranging from 0 to 3, representing the number of GCMs predicting each grid cell as suitable. Suitable-area extent was calculated for each suitability class using latitude-adjusted grid-cell areas. Areas were also calculated separately for each GCM, and the mean, standard deviation, minimum, and maximum were summarized for each SSP scenario. These statistics were used to describe variation among GCM projections rather than total uncertainty in future species distributions. Changes between current and future climatic suitability were assessed after converting the current and future ensemble projections into binary maps, with poorly, moderately, and highly suitable classes treated as suitable. Grid cells were classified as stable unsuitable, suitable-area loss, newly suitable, or stable suitable. The corresponding areas, net change, retention rate, and loss rate were calculated for each SSP scenario. For newly suitable areas, the GCM agreement index was used to quantify the areas supported by one, two, or all three GCMs and the proportion supported by at least two models.

### 3. Results

#### 3.1. Model Optimization and Performance

A total of 48 candidate models combining six feature-class settings and eight regularization multipliers were evaluated using four-fold spatial block cross-validation. Model performance varied among parameter combinations, indicating that model complexity substantially affected predictive accuracy and transferability. Based on the joint consideration of validation AUC, omission rate, continuous Boyce index and model complexity, the model combining linear, quadratic, hinge and product features with a regularization multiplier of 0.5 was selected as the optimal parameterization. The selected model achieved a mean validation AUC of  $0.853 \pm 0.138$  and a mean 10th-percentile omission rate of  $0.222 \pm 0.265$ . The mean validation CBI was  $0.732 \pm 0.297$ , whereas the mean training CBI was  $0.985 \pm 0.008$  (Table 3). These results indicated generally good discriminatory and ranking performance, while the variation among spatial folds reflected spatial heterogeneity in predictive transferability.

**Table 3.** Parameter settings and spatial cross-validation performance of the selected MaxEnt model for *C. officinalis*.

| Category               | Metric or Parameter              | Selected Model/Value    |
|------------------------|----------------------------------|-------------------------|
| Model configuration    | Feature classes                  | LQHP                    |
|                        | Regularization multiplier        | 0.5                     |
| Candidate-model search | Parameter combinations evaluated | 48                      |
| Calibration data       | Occurrence records               | 381                     |
|                        | Background points                | 10,000                  |
| Cross-validation       | Partitioning method              | Four-fold spatial block |
| Predictive performance | Validation AUC                   | $0.853 \pm 0.138$       |
| Omission error         | OR10                             | $0.222 \pm 0.265$       |
| Ranking performance    | Validation CBI                   | $0.732 \pm 0.297$       |
|                        | Training CBI                     | $0.985 \pm 0.008$       |

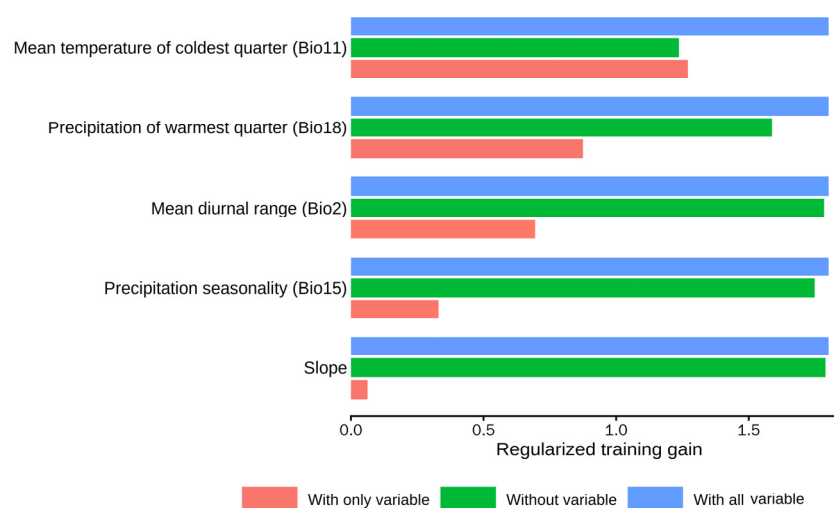
#### 3.2. Environmental Contributions and Response Patterns

The five environmental predictors differed substantially in their contributions to the final MaxEnt model (Table 4). Mean temperature of the coldest quarter (Bio11) had the highest percentage contribution (59.040%) and permutation importance (75.420%), followed by precipitation of the warmest quarter (Bio18), with a contribution of 33.490% and a permutation importance of 17.340%. Together, Bio11 and Bio18 accounted for 92.53% of the total model contribution and 92.76% of the total permutation importance. Mean diurnal temperature range (Bio2), precipitation seasonality (Bio15), and slope made relatively limited contributions, accounting for 3.760%, 2.700%, and 1.010% of the model contribution, respectively.

The Jackknife test further highlighted the importance of Bio11 (Figure 2). When used alone, Bio11 produced the highest regularized training gain (1.271), indicating that it contained the greatest amount of independently useful information. Bio18 produced the second-highest training gain when used alone (0.875). Omitting Bio11 reduced the training gain of the full model from 1.801 to 1.237, representing the largest reduction among the predictors and indicating that Bio11 contained substantial information not captured by the other variables. Omitting Bio18 also reduced the training gain to 1.588, whereas omission of Bio2, Bio15, or slope caused comparatively small reductions.

**Table 4.** Relative importance of environmental predictors in the final MaxEnt model for *C. officinalis*.

| Environment Variable | Percent Contribution | Permutation Importance | Gain When Used Alone | Gain When Omitted |
|----------------------|----------------------|------------------------|----------------------|-------------------|
| Bio11                | 59.040               | 75.420                 | 1.271                | 1.237             |
| Bio18                | 33.490               | 17.340                 | 0.875                | 1.588             |
| Bio2                 | 3.760                | 1.970                  | 0.695                | 1.784             |
| Bio15                | 2.700                | 4.310                  | 0.331                | 1.748             |
| Slope                | 1.010                | 0.960                  | 0.063                | 1.789             |

**Figure 2.** Jackknife test of environmental variable importance.

Single-variable response curves showed nonlinear relationships between the predictors and cloglog suitability (Figure 3). Bio11 displayed a unimodal response, peaking at approximately  $-1.7^{\circ}\text{C}$ , with cloglog suitability values of at least 0.5 occurring mainly between approximately  $-3.7$  and  $4.0^{\circ}\text{C}$ . Bio18 showed a similar unimodal pattern, reaching its maximum at approximately 752 mm, with values of at least 0.5 occurring between approximately 565 and 835 mm. Suitability associated with Bio2 peaked at approximately  $9.7^{\circ}\text{C}$ , and values of at least 0.5 occurred mainly between approximately  $8.3$  and  $11.0^{\circ}\text{C}$ . The response to Bio15 was more irregular, with several local increases in suitability, indicating a less clearly defined univariate relationship. The 0.5 value was used only as a descriptive reference for relatively high modeled suitability and should not be interpreted as an ecological threshold or an absolute probability of occurrence.

### 3.3. Current Climatic Suitability and Spatial Distribution

Under current climatic conditions, the potential suitable habitat of *C. officinalis* was concentrated mainly in the temperate regions of East Asia, with additional isolated suitable areas in eastern North America and Europe (Figure 4). In East Asia, the largest continuous suitable region extended across central and eastern China, the Korean Peninsula, and Japan. However, suitability levels differed markedly within this region. Poorly suitable habitat dominated much of central and eastern China, with scattered moderately suitable areas and only limited highly suitable patches. In contrast, extensive highly suitable habitat was predicted across the Korean Peninsula, while moderate- and high-suitability areas were also widely distributed along the Japanese archipelago. Narrow and discontinuous suitable areas additionally occurred along the southern margin of the Qinghai–Tibet Plateau and the Himalayan region.

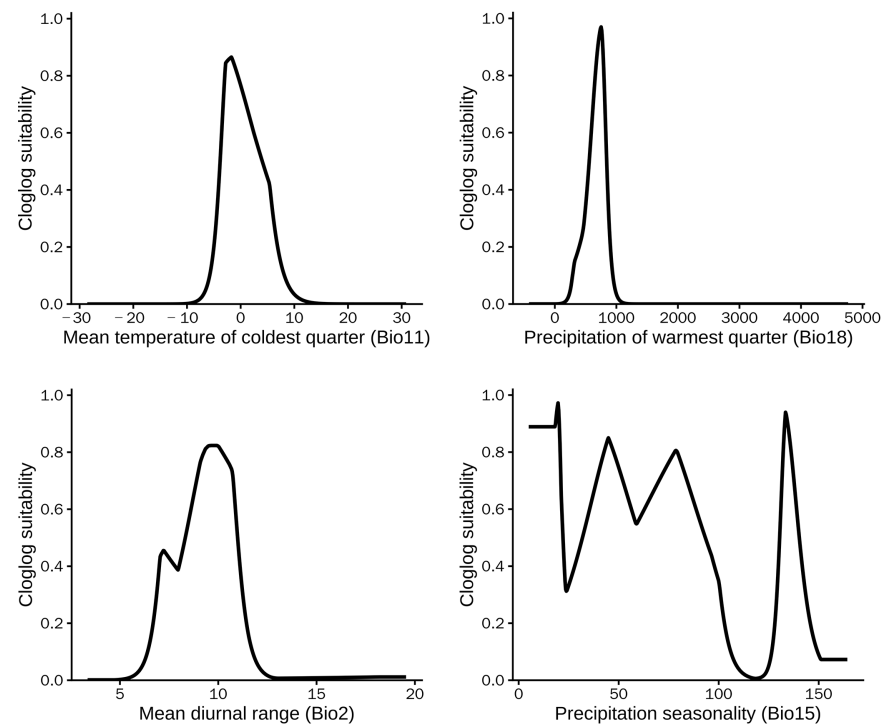


**Figure 3.** Single-factor response curves of the dominant environmental variables.

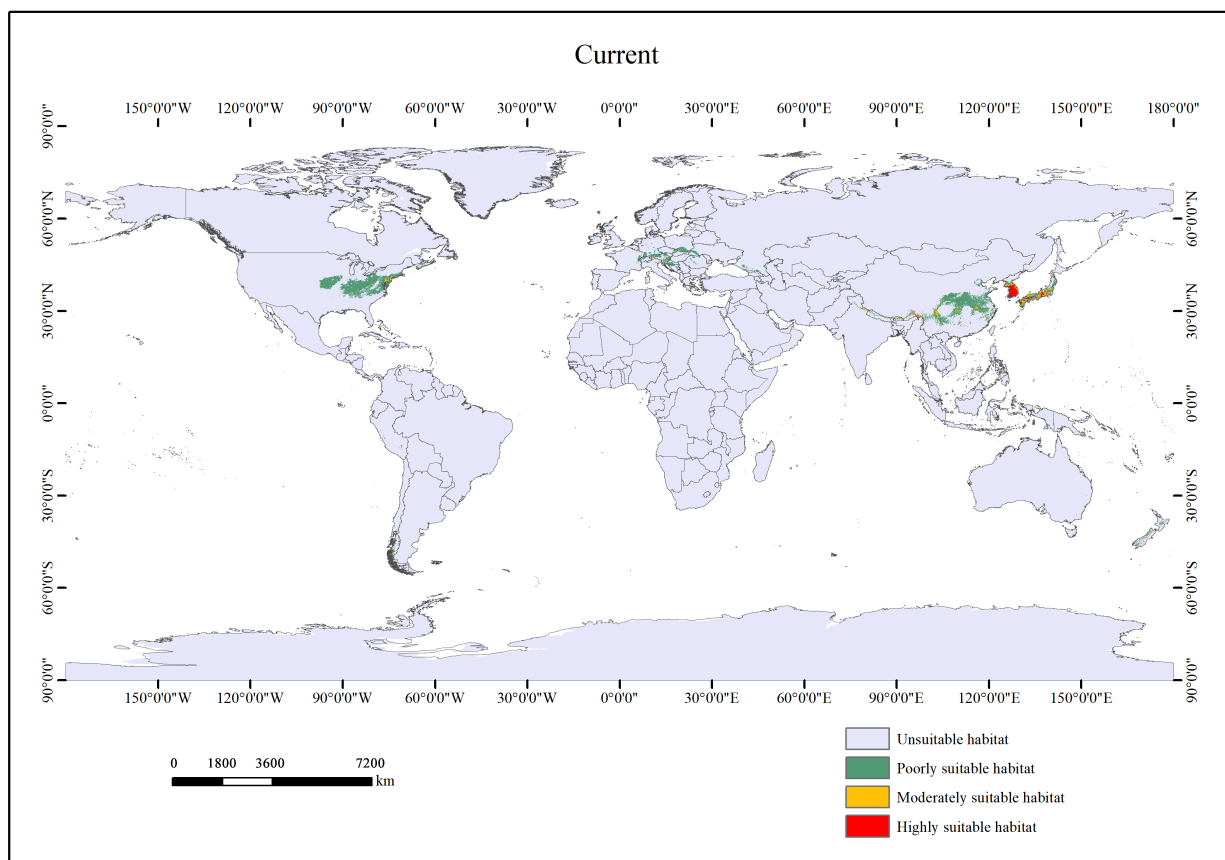


**Figure 4.** Climatically suitable areas for *C. officinalis* under current climate conditions.

Outside East Asia, suitable habitats were considerably more restricted and fragmented. In eastern North America, poorly suitable habitat occurred mainly across parts of the

eastern and central United States, with a small concentration of moderate to high suitability near the northeastern Atlantic coast. In Europe, suitable habitats were predominantly classified as poorly suitable and occurred as scattered patches across parts of central and southeastern Europe, with additional limited areas near the Caucasus region. These extralimital predictions were dominated by low-suitability classes and lacked the extensive high-suitability zones observed in the Korean Peninsula and Japan.

Based on the 10th-percentile training presence threshold, areas with cloglog suitability values of at least 0.209 were considered climatically suitable for *C. officinalis*. Within the global projection extent, the total suitable area was approximately  $277.247 \times 10^4 \text{ km}^2$ . Low-suitability habitat accounted for the largest proportion, covering  $241.153 \times 10^4 \text{ km}^2$  and representing 86.980% of the total suitable area. Moderate- and high-suitability habitats covered  $23.373 \times 10^4$  and  $12.721 \times 10^4 \text{ km}^2$ , respectively, accounting for 8.430% and 4.590% of the total suitable area (Table 5).

**Table 5.** Areas and proportions of current climatic suitability classes for *C. officinalis* at the global scale.

| Suitability Class        | Cloglog Range | Area ( $10^4 \text{ km}^2$ ) | Percentage of Suitable Area (%) |
|--------------------------|---------------|------------------------------|---------------------------------|
| Poorly suitable area     | 0.209–<0.473  | 241.153                      | 86.980                          |
| Moderately suitable area | 0.473–<0.736  | 23.373                       | 8.430                           |
| Highly suitable area     | $\geq 0.736$  | 12.721                       | 4.590                           |
| Total suitable area      | $\geq 0.209$  | 277.247                      | 100.000                         |

3.4. Distribution and Dynamics of Global Climatically Suitable Areas Under Paleoclimatic Conditions

The predicted climatically suitable area of *C. officinalis* changed substantially across paleoclimatic periods and generally expanded toward the present (Figure 5). Total suitable area increased from  $164.050 \times 10^4 \text{ km}^2$  during the Last Interglacial to  $229.580 \times 10^4 \text{ km}^2$  during the Last Glacial Maximum and  $275.220 \times 10^4 \text{ km}^2$  during the Mid-Holocene, reaching  $277.247 \times 10^4 \text{ km}^2$  under current climatic conditions (Figure 5D). Spatially, suitable habitats were consistently concentrated in East Asia, particularly in eastern and central China, the Korean Peninsula, and Japan, with smaller and more fragmented suitable areas occurring in eastern North America, Europe, southern South America, southeastern Australia, and New Zealand (Figure 5A–C). The temporal increase in total suitable area was driven mainly by the expansion of poorly suitable habitat, which rose from  $121.890 \times 10^4 \text{ km}^2$  during the Last Interglacial to  $241.153 \times 10^4 \text{ km}^2$  at present. Moderately suitable habitat increased from  $30.630 \times 10^4 \text{ km}^2$  during the Last Interglacial to a maximum of  $48.510 \times 10^4 \text{ km}^2$  during the Last Glacial Maximum, but subsequently declined to  $23.373 \times 10^4 \text{ km}^2$  under current conditions. In contrast, highly suitable habitat varied comparatively little among periods, ranging from  $11.530 \times 10^4$  to  $14.890 \times 10^4 \text{ km}^2$ . These results indicate that the historical expansion of climatically suitable habitat was dominated by increases in low-suitability areas rather than by a sustained expansion of highly suitable habitat.

3.5. Future Climatic Suitability Under Different SSP Scenarios

Ensemble projections based on ACCESS-CM2, BCC-CSM2-MR and CMCC-ESM2 indicated that climatically suitable areas for *C. officinalis* during 2081–2100 were mainly distributed in East Asia, eastern North America and parts of Europe under all four SSP scenarios (Figure 6). In East Asia, suitable habitats were concentrated in eastern and central China, the Korean Peninsula and Japan, with the most highly suitable areas occurring mainly in eastern China, southern Korea and Japan. Additional poorly to moderately suitable areas were projected in the eastern United States and southeastern Canada, whereas scattered suitable habitats occurred in western and central Europe.

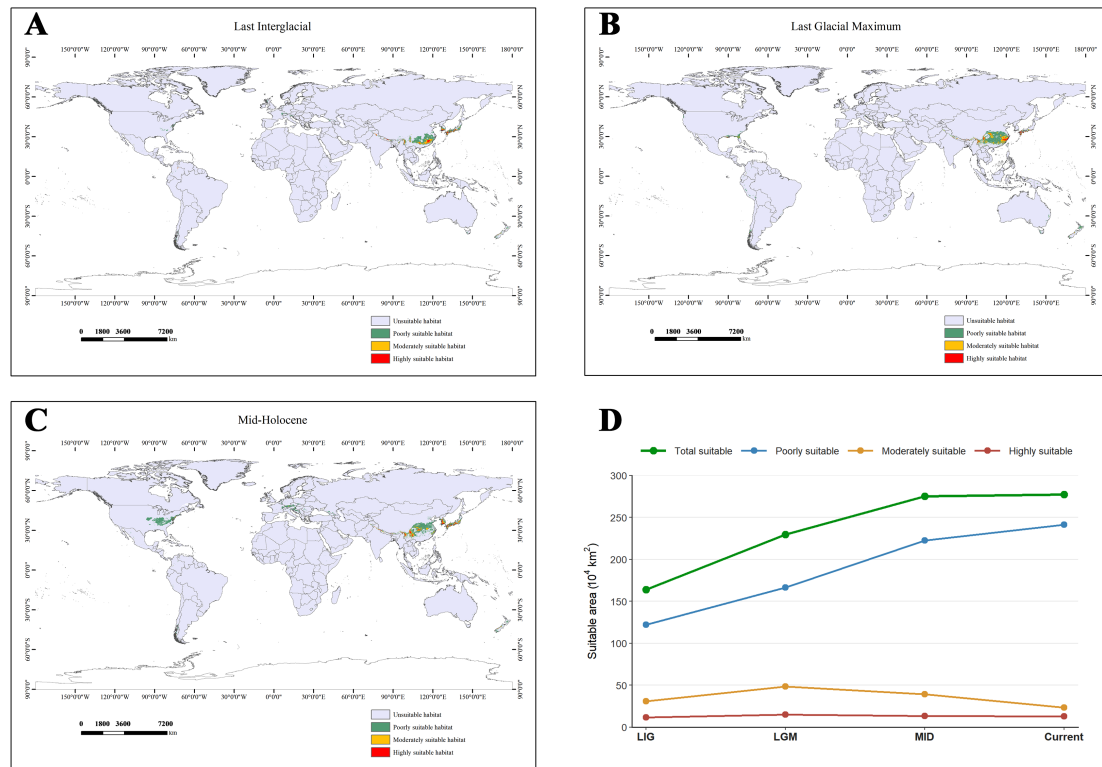


**Figure 5.** Predicted climatically suitable areas of *C. officinalis* during paleoclimatic periods and temporal changes in suitable-area extent. (A) Last Interglacial; (B) Last Glacial Maximum; (C) Mid-Holocene; and (D) changes in the areas of poorly, moderately, highly, and total suitable habitats from the Last Interglacial to the current period.

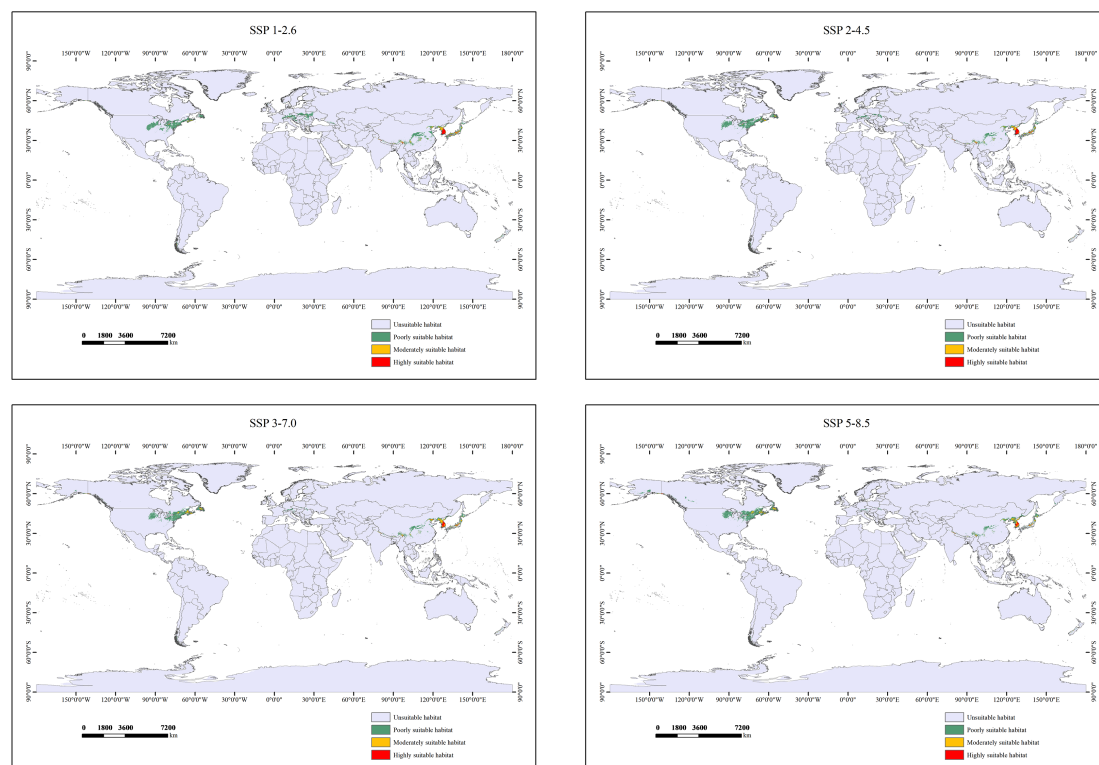


**Figure 6.** Ensemble projections of the future climatic suitability of *C. officinalis* during 2081–2100 under four SSP scenarios.

The spatial extent of suitable habitat differed among emission scenarios. SSP1-2.6 produced the broadest ensemble-predicted suitable area, particularly across eastern North America, Europe and East Asia. Suitable habitat contracted under SSP2-4.5 and SSP3-7.0, with SSP3-7.0 showing the smallest total suitable area. Under SSP5-8.5, the total suitable area increased slightly relative to SSP3-7.0, mainly because of an expansion of poorly suitable habitat, while highly suitable habitat continued to decline.

The ensemble-classified total suitable area was  $243.689 \times 10^4 \text{ km}^2$  under SSP1-2.6, decreasing to  $206.615 \times 10^4 \text{ km}^2$  under SSP2-4.5 and  $201.393 \times 10^4 \text{ km}^2$  under SSP3-7.0, and then increasing slightly to  $206.168 \times 10^4 \text{ km}^2$  under SSP5-8.5. Poorly suitable habitat accounted for the largest proportion under all scenarios, ranging from  $165.804 \times 10^4 \text{ km}^2$  under SSP3-7.0 to  $210.651 \times 10^4 \text{ km}^2$  under SSP1-2.6. Moderately suitable habitat ranged from 20.488 to  $27.331 \times 10^4 \text{ km}^2$ . Highly suitable habitat was relatively stable under SSP1-2.6 and SSP2-4.5, at  $11.681$  and  $11.875 \times 10^4 \text{ km}^2$ , respectively, but declined to  $8.259 \times 10^4 \text{ km}^2$  under SSP3-7.0 and  $6.225 \times 10^4 \text{ km}^2$  under SSP5-8.5 (Table 6).

**Table 6.** Ensemble-predicted suitable habitat areas and inter-model variation for *C. officinalis* during 2081–2100 under four SSP scenarios.

| Scenario | Poorly Suitable Habitat | Moderately Suitable Habitat | Highly Suitable Habitat | Total Suitable Habitat | Mean Area $10^4 \text{ km}^2$ | Sd Area $10^4 \text{ km}^2$ | Min Area $10^4 \text{ km}^2$ | Max Area $10^4 \text{ km}^2$ |
|----------|-------------------------|-----------------------------|-------------------------|------------------------|-------------------------------|-----------------------------|------------------------------|------------------------------|
| SSP1-2.6 | 210.651                 | 21.357                      | 11.681                  | 243.689                | 250.668                       | 28.226                      | 219.978                      | 275.51                       |
| SSP2-4.5 | 174.253                 | 20.488                      | 11.875                  | 206.615                | 213.969                       | 30.140                      | 179.560                      | 235.690                      |
| SSP3-7.0 | 165.804                 | 27.331                      | 8.259                   | 201.393                | 213.133                       | 22.287                      | 191.061                      | 235.629                      |
| SSP5-8.5 | 175.447                 | 24.496                      | 6.225                   | 206.168                | 216.882                       | 40.947                      | 189.132                      | 263.909                      |

Notes: Poorly, moderately, highly and total suitable areas were calculated from the classified ensemble-mean predictions. Mean, standard deviation, minimum and maximum values represent variation in total suitable area among ACCESS-CM2, BCC-CSM2-MR and CMCC-ESM2.

### 3.6. Inter-Model Agreement and Uncertainty Among GCMs

Agreement among ACCESS-CM2, BCC-CSM2-MR and CMCC-ESM2 varied spatially across the four SSP scenarios (Figure 7). Areas consistently predicted as suitable by all three GCMs were mainly concentrated in East Asia and eastern North America, particularly eastern China, the Korean Peninsula, Japan and parts of the eastern suitable range in North America. In contrast, predictions in Europe were more fragmented and were often supported by only one or two GCMs. Lower agreement generally occurred near the margins of projected suitable areas, suggesting that these peripheral predictions were more sensitive to the choice of climate model.

Inter-model standard deviation was generally low across most terrestrial regions, while locally elevated values occurred mainly within or around projected suitable areas in East Asia, eastern North America and parts of Europe (Figure 8). These higher-SD regions were often associated with the boundaries of suitable habitats, whereas core suitable areas tended to show lower variation among GCMs. The broad spatial pattern was similar among SSP scenarios, although local differences remained.

Variation in total suitable area was greatest under SSP5-8.5, with a mean of  $216.882 \pm 40.947 \times 10^4 \text{ km}^2$  and a range of  $189.132\text{--}263.909 \times 10^4 \text{ km}^2$ . The smallest standard deviation occurred under SSP3-7.0, with a mean of  $213.133 \pm 22.287 \times 10^4 \text{ km}^2$ . Overall, the three GCMs showed broadly comparable geographical patterns, although uncertainty was relatively greater in some peripheral and spatially fragmented regions (Table 6).

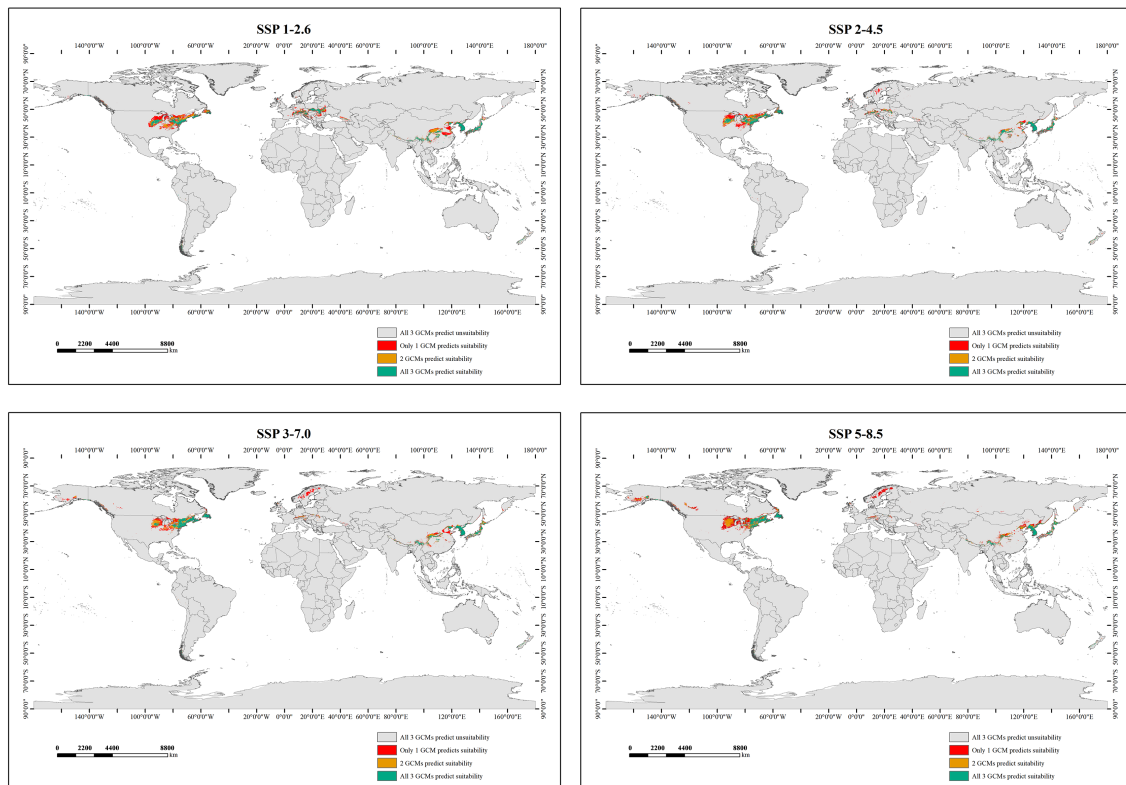


**Figure 7.** Agreement among three global climate models in predicting future climatically suitable areas for *C. officinalis* during 2081–2100.

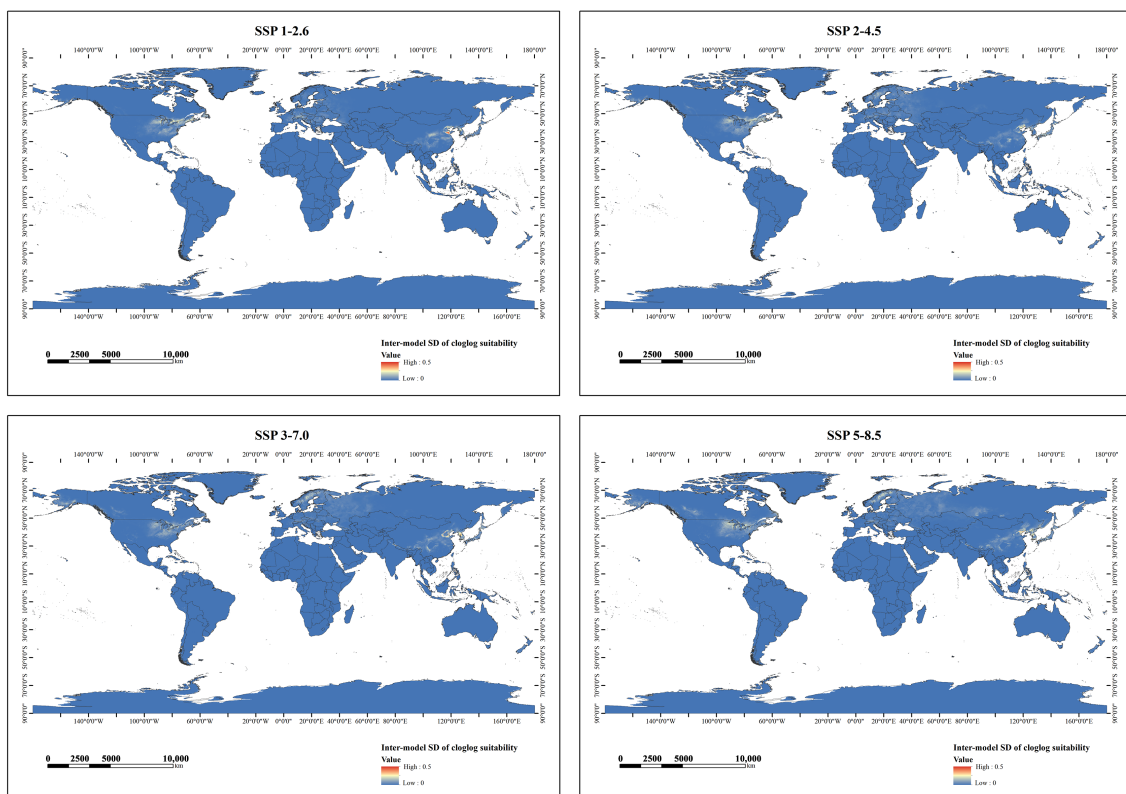


**Figure 8.** Spatial variation in inter-model uncertainty of projected climatic suitability for *C. officinalis* during 2081–2100 under four SSP scenarios.

### 3.7. Current-to-Future Shifts in Climatically Suitable Areas

Comparison of the current and future ensemble projections indicated substantial spatial redistribution of climatically suitable areas for *C. officinalis* under all four SSP scenarios (Figure 9). Suitable areas generally contracted in central China, the southern United States and southern Japan across all scenarios. Europe also showed considerable habitat loss under SSP2-4.5, SSP3-7.0 and SSP5-8.5, whereas this contraction was less apparent under SSP1-2.6. In contrast, suitable areas on the Korean Peninsula remained comparatively stable. Newly suitable areas generally occurred north of the current suitable range, indicating a northward shift in parts of China, the United States, Japan and Europe.

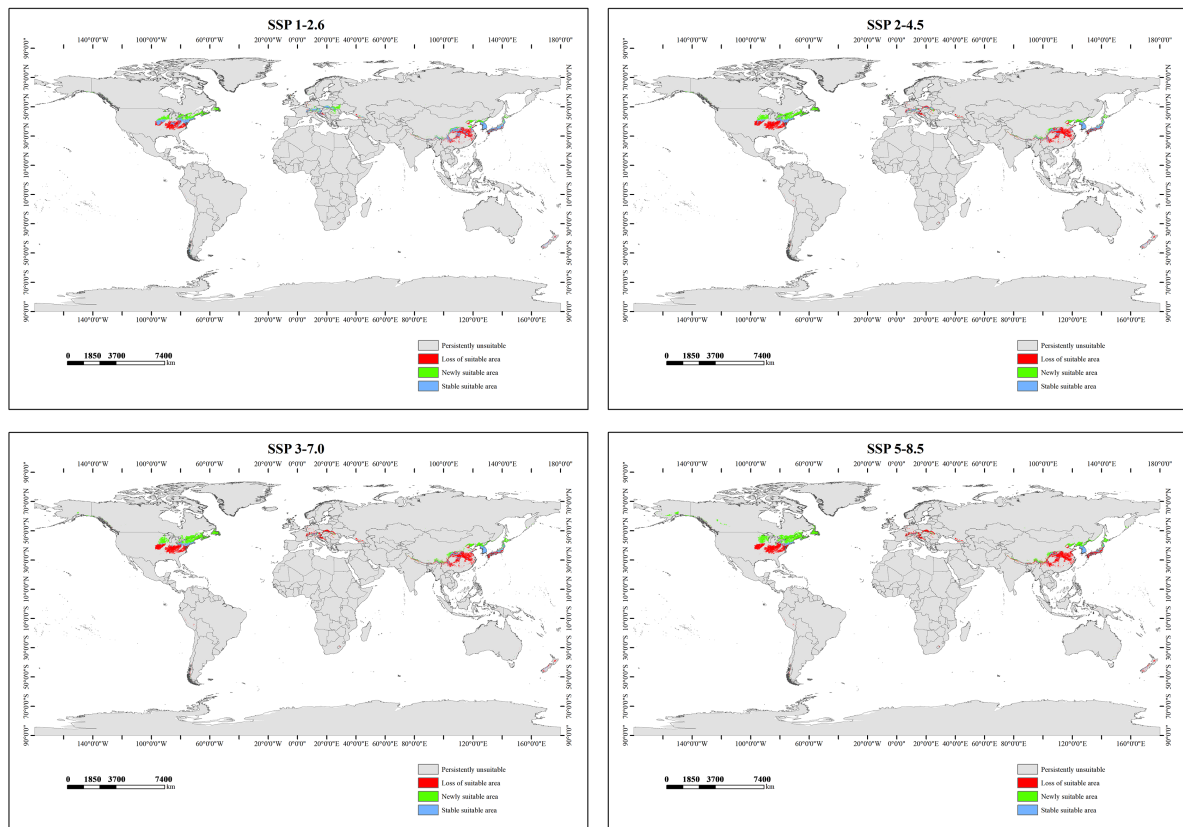


**Figure 9.** Current-to-future shifts in climatically suitable areas of *C. officinalis* under four SSP scenarios.

The spatial redistribution was accompanied by increasing loss of existing suitable habitat. Stable suitable area declined from  $146.600 \times 10^4 \text{ km}^2$  under SSP1-2.6 to  $54.720 \times 10^4 \text{ km}^2$  under SSP5-8.5, while habitat loss increased from  $130.648$  to  $222.530 \times 10^4 \text{ km}^2$ . Newly suitable area also increased, from  $97.090 \times 10^4 \text{ km}^2$  under SSP1-2.6 to  $151.450 \times 10^4 \text{ km}^2$  under SSP5-8.5. However, gains were smaller than losses under every scenario, resulting in net reductions of  $33.558\text{--}75.854 \times 10^4 \text{ km}^2$ . The largest net decline occurred under SSP3-7.0, whereas SSP5-8.5 showed the lowest retention of current suitable habitat.

Most newly suitable areas were supported by at least two of the three GCMs (Figure 10). Majority-supported gains accounted for  $81.390, 97.600, 116.200$  and  $134.648 \times 10^4 \text{ km}^2$  under SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5, respectively, corresponding to 83.800–92.700% of the total gained area. Areas supported by all three GCMs increased from  $38.430 \times 10^4 \text{ km}^2$  under SSP1-2.6 to  $76.820 \times 10^4 \text{ km}^2$  under SSP5-8.5. Overall, the projections suggest substantial future reorganization of climatic suitability, characterized by losses within parts of the current range and the emergence of new potential habitats farther north.

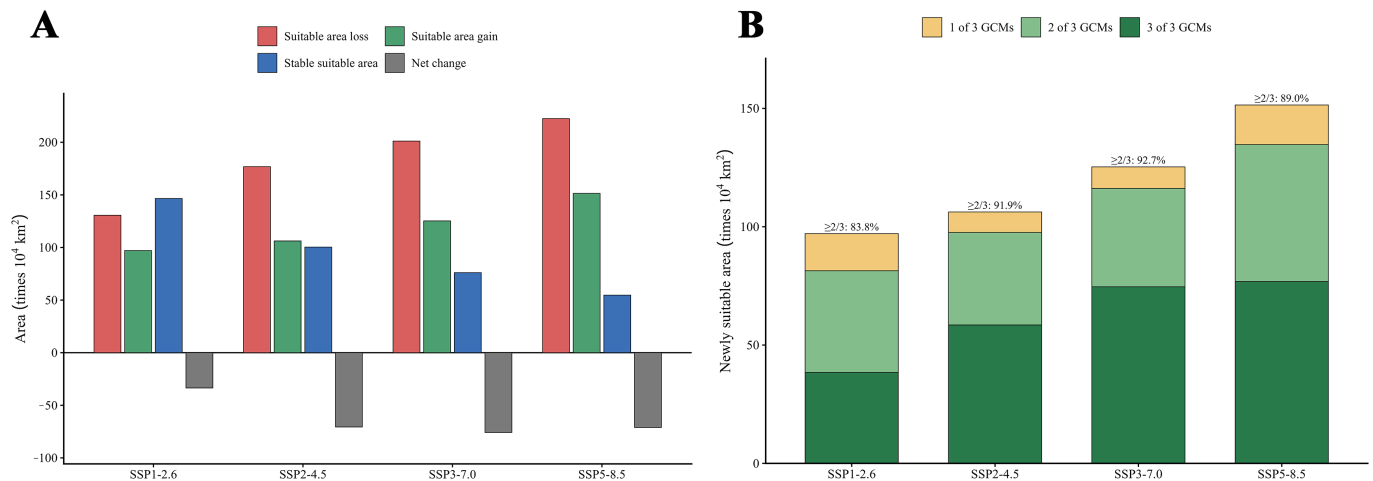


**Figure 10.** Suitable-area changes and inter-model support for projected habitat gains under four SSP scenarios. (A) Areas of suitable habitat loss, gain, persistence, and net change relative to the current period. (B) Newly suitable areas supported by one, two, or all three GCMs under four SSP scenarios.

## 4. Discussion

### 4.1. Model Performance and Robustness of Climatic Suitability Projections

The performance of the 48 candidate models varied substantially with feature-class combinations and regularization strength, confirming that MaxEnt predictions were sensitive to model complexity. Default settings therefore may not provide the most appropriate balance between fit and transferability for a given species [37]. Models with excessive flexibility can reproduce local patterns in the calibration data but perform less reliably when transferred across regions or climatic periods, whereas overly strong regularization may suppress ecologically meaningful responses [32]. Species-specific tuning is thus particularly important when models are projected to paleoclimatic and future conditions [38]. The selected LQHP model with a regularization multiplier of 0.5 retained nonlinear and interactive environmental responses while avoiding the threshold feature, which can produce abrupt response boundaries. Because AUC and CBI measure different aspects of predictive performance, neither metric alone was treated as definitive evidence of model reliability. However, the lower validation CBI relative to the training value, together with the relatively large variation among folds, suggests that predictive transferability differed among geographic sectors. This likely reflects spatial heterogeneity in the occurrence records and environmental conditions rather than a uniform level of model performance across the study area. The use of four-fold spatial block cross-validation provided a more stringent evaluation than random partitioning because geographically close records were less likely to occur simultaneously in the calibration and validation subsets. Random partitioning can overestimate predictive performance when nearby records share similar environmental conditions, whereas spatially structured validation is better suited to evaluating transfer to unsampled regions and future climates [28]. In this study, validation AUC, OR10 and CBI were considered jointly because they describe complementary aspects of model performance. Overall, model tuning and spatial validation provided a stronger basis for broad-scale climatic suitability projections, although fold-level variation indicates that the predictions should not be interpreted as equally precise across all regions.

#### 4.2. Environmental Controls on the Climatic Suitability of *C. officinalis*

The strong contributions of Bio11 and Bio18 indicate that the climatic suitability of *C. officinalis* is primarily associated with winter thermal conditions and water availability during the warmest part of the year. Mean temperature of the coldest quarter contributed the greatest amount of unique information to the model, suggesting that cold-season temperature represents a major climatic constraint on the species' distribution. For temperate deciduous woody plants, winter temperature can influence tissue survival, dormancy progression and subsequent spring development, thereby affecting the geographical limits within which populations can persist [39,40]. The unimodal response to Bio11 further indicates that suitability was associated with an intermediate winter-temperature range rather than increasing continuously with warmer conditions. This modeled association may reflect the combined effects of cold injury under severe winters and insufficient chilling under comparatively mild winters, although these mechanisms were not directly evaluated for *C. officinalis*.

Bio18 was the second most influential predictor, showing that precipitation during the warmest quarter also plays an important role in defining suitable climatic conditions. This period generally overlaps with active vegetative growth and high evaporative demand, so insufficient rainfall may increase seasonal water limitation. Warm-season moisture availability commonly affects woody-plant growth and survival through its influence on plant water status and hydraulic function [41,42]. However, the unimodal response indicates that higher precipitation was not uniformly associated with greater suitability. Excessively wet conditions may alter soil aeration, drainage and local moisture balance, although these mechanisms were not directly tested in the present study. The combined importance of Bio11 and Bio18 therefore points to a seasonal water–temperature balance rather than control by either temperature or precipitation alone. Similar combinations of cold-season temperature and growing-season moisture have frequently been identified as important determinants of woody-plant distributions in temperate and monsoon-influenced regions [42,43]. Bio2, Bio15 and slope made smaller contributions, but this does not necessarily mean that they are ecologically unimportant. Mean diurnal temperature range and precipitation seasonality may refine the climatic niche by representing short-term temperature fluctuations and the annual distribution of rainfall. Their additional contribution was limited after Bio11 and Bio18 had already captured most of the model information. Slope may indirectly reflect differences in drainage, exposure and local microclimate rather than acting as a direct physiological constraint [44]. Moreover, because the response curves were generated from single-variable models, the estimated peaks and favorable ranges should be interpreted as descriptive associations within the calibration data, not as experimentally verified physiological thresholds. Overall, the model suggests that *C. officinalis* is associated with a relatively specific combination of winter temperature and warm-season precipitation, with secondary modification by climatic variability and terrain.

#### 4.3. Current and Paleoclimatic Patterns of Climatic Suitability

The present-day projection places the main climatic suitability of *C. officinalis* in East Asia, particularly across central and eastern China, the Korean Peninsula, and Japan. This pattern is consistent with its known biogeographic affinity and with previous China-scale predictions that identified east-central China as a principal suitable region [5]. However, most of the globally predicted suitable area was classified as poorly suitable, indicating that climatically analogous space is considerably broader than the core climatic niche. The larger moderate- and high-suitability areas in the Korean Peninsula and Japan may reflect more favorable combinations of winter temperature and warm-season precipitation, whereas the predominance of low suitability across much of China suggests marked climatic heterogene-

ity within the main East Asian region. The scattered predictions in eastern North America and Europe require more cautious interpretation. Because these areas were largely poorly suitable and geographically isolated from the known distribution, they are better regarded as climatic analogues than as evidence of current occurrence or immediate cultivation potential. Correlative models do not explicitly incorporate dispersal history, biotic interactions, or establishment barriers, all of which may restrict realized distributions even where climate appears suitable [45]. Across paleoclimatic periods, suitable areas remained centered on East Asia but varied substantially in extent and composition. The smaller suitable area during the Last Interglacial and the expansion during the Last Glacial Maximum indicate that responses were not determined by temperature alone. Given the dominant roles of cold-quarter temperature and warm-quarter precipitation, historical suitability may have reflected changes in their regional combination, including glacial–interglacial variation in East Asian monsoon conditions. Palaeoclimatic studies have documented substantial changes in East Asian temperature, precipitation, and monsoon intensity across glacial–interglacial periods, although the present model does not directly identify the mechanisms responsible for the projected changes [46,47]. Importantly, the increase in total suitable area toward the present was driven mainly by poorly suitable habitat, while highly suitable area remained relatively stable. Thus, historical expansion should not be interpreted as a corresponding enlargement of the climatic core. Instead, it suggests that marginal climatic space expanded around a more limited set of favorable regions. The persistent concentration of suitable areas in East Asia indicates modeled climatic stability across the evaluated periods, but it does not by itself demonstrate long-term population persistence or the presence of historical refugia. Identifying refugia generally requires integration of distribution models with fossil, palaeoecological, or phylogeographic evidence [48,49].

#### 4.4. Future Climatic Suitability and Inter-Model Variation

Future projections indicate that the broad climatic suitability pattern of *C. officinalis* would remain centred on East Asia, with secondary suitable regions in eastern North America and Europe. However, total suitable area decreased from SSP1-2.6 to the higher-emission scenarios. The slight increase under SSP5-8.5 relative to SSP3-7.0 was driven mainly by poorly suitable habitat, while highly suitable area continued to decline. This result indicates that changes in total suitable area may conceal shifts toward lower suitability classes, especially when gains occur mainly near the classification threshold. The marked reduction in highly suitable habitat under SSP3-7.0 and SSP5-8.5 suggests contraction of the climatic core under stronger climate forcing. By contrast, SSP1-2.6 retained a broader suitable area, indicating that lower-emission pathways may preserve more climatic space associated with the species. Even so, poorly suitable habitat dominated under all scenarios, so future change is better interpreted as a redistribution and weakening of climatic suitability than as simple range expansion or contraction. The three GCMs produced broadly similar patterns in East Asia and eastern North America, supporting the robustness of these large-scale signals. Agreement was lower in Europe and near suitability margins, where predictions were often supported by only one or two models and inter-model SD was locally higher. Predictions near class boundaries are particularly sensitive to relatively small differences among climate models because these differences can shift grid cells between suitable and unsuitable categories. These fragmented predictions should therefore be interpreted more cautiously than areas consistently supported by all three models. Inter-model variation was greatest under SSP5-8.5, but did not increase consistently with emission intensity, indicating that uncertainty depended on the regional climatic responses of individual GCMs rather than on scenario strength alone. GCM selection is an important source of variation in species-distribution projections, and reliance on a single model may overlook

alternative outcomes [36,50]. Multi-model ensembles can provide a more representative central projection and help characterize climate-model uncertainty [50,51]. However, ensemble averaging does not eliminate disagreement among models and may obscure locally divergent projections if measures of model spread are not also reported. Accordingly, the ensemble mean, agreement count and inter-model SD provide complementary evidence for evaluating future climatic suitability.

#### 4.5. Current-to-Future Redistribution of Climatic Suitability

Future change in *C. officinalis* is characterized by spatial reorganization rather than uniform contraction. Suitable areas were projected to decline in central China, the southern United States and southern Japan, while newly suitable areas generally appeared farther north in China, North America, Japan and Europe. This pattern is consistent with the broader tendency for climatic suitability to shift poleward under warming, although responses vary among species and regions [52,53]. The Korean Peninsula remained comparatively stable, suggesting that some regions may retain favorable combinations of winter temperature and warm-season precipitation. Both habitat loss and gain increased under stronger scenarios, but gains remained smaller than losses in every case. Thus, net area alone does not fully describe future change. The low retention of current suitable habitat under SSP5-8.5 indicates that much of the present climatic space may be lost even as new climatic analogues emerge elsewhere. These newly suitable areas are not direct replacements for lost regions, particularly when they are distant from current populations or cultivation centres. Most gained areas were supported by at least two GCMs, indicating that the northward expansion signal was not driven by a single climate model. However, model agreement reflects consistency in climatic suitability rather than actual colonization potential. For a long-lived woody species, dispersal, establishment and population development may lag behind the rate of climatic change [43]. Areas projected to remain suitable across scenarios may therefore deserve priority for germplasm conservation and long-term cultivation planning, whereas repeatedly lost areas warrant closer monitoring. Newly suitable regions supported by multiple GCMs could be considered for field evaluation or experimental introduction, but should not be treated directly as established cultivation zones. Any translocation beyond the current range would also require careful assessment of establishment success and potential ecological risks [54].

#### 4.6. Implications for Climate-Informed Planning and Study Limitations

The spatially stable suitable areas identified across climatic periods and future scenarios provide a useful basis for prioritizing germplasm conservation, long-term monitoring and climate-informed cultivation planning. In particular, regions projected to retain moderate or high climatic suitability may represent comparatively stable climatic settings for maintaining existing resources. However, model-based priority areas should be regarded as candidates for further assessment rather than direct management prescriptions, because species-distribution projections may not fully represent local ecological conditions or future changes in occupancy [55,56]. Newly suitable areas supported by two or all three GCMs may also warrant field investigation and experimental introduction, whereas regions showing repeated losses of current suitability should receive greater attention in future climate-risk assessments [57]. These projections are therefore most useful for identifying broad priority regions rather than prescribing specific cultivation sites. The results should nevertheless be interpreted within the scope of the modelling framework. Because Max-Ent infers suitability from correlations between presence records and climate rather than from mechanistic processes, it does not by itself forecast establishment, yield or product quality [58]. In addition, the global extent and approximately 5 km spatial resolution

are appropriate for regional screening but cannot resolve local site conditions. Although the use of three GCMs and spatially structured model evaluation reduced reliance on a single projection, uncertainty associated with climate scenarios, inter-model differences and temporal transfer remains [59]. Clamping was applied during projection to constrain model responses under environmental conditions beyond the calibration range; nevertheless, the most distant future projections extend into climatic space that is poorly represented in the calibration data, where suitability estimates rely on extrapolation and are therefore least certain. Accordingly, the identified suitable regions should be regarded as a climatic basis for subsequent field evaluation rather than definitive cultivation zones. Overall, this study provides a consistent assessment of the climatic suitability of *C. officinalis* from paleoclimatic periods to the end of the twenty-first century, while explicitly distinguishing changes in suitability level, spatial persistence and agreement among climate models.

## 5. Conclusions

This study developed an optimized MaxEnt model to assess the climatic suitability of *C. officinalis* from paleoclimatic periods to the end of the twenty-first century. Cold-quarter temperature and warm-season precipitation were the dominant environmental constraints, and East Asia remained the principal suitable region across all periods. Future projections indicated substantial spatial redistribution, with losses in parts of the current suitable range and newly suitable areas emerging mainly farther north. Because gains did not offset losses under any SSP scenario, climate change is likely to reduce and reorganize suitable climatic space, particularly under stronger forcing. The identified stable and multi-model-supported regions provide a climatic basis for germplasm conservation, long-term monitoring and future cultivation planning.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae12080989/s1>, Table S1: Spatially filtered occurrence records of *Cornus officinalis* used for MaxEnt modelling; Table S2: Current-to-future changes in climatically suitable areas under the four SSP scenarios; Table S3: Areas of climatically suitable habitat under current, historical, and future climate scenarios; Table S4: Ensemble statistics of climatically suitable areas across three GCMs under each SSP scenario; Table S5: Detailed GCM agreement for newly suitable areas under future climate scenarios; Table S6: Summary of GCM agreement for newly suitable areas under future climate scenarios; Table S7: Areas of newly suitable habitat supported by one, two, or three GCMs; Table S8: Mean, standard deviation, minimum, and maximum suitable areas predicted by individual GCMs; Table S9: MaxEnt model outputs and evaluation statistics for the final optimized model; Data S1: Accessible calibration area (M) used for MaxEnt model calibration.

**Author Contributions:** Conceptualization, T.Z. and W.S.; methodology, T.Z. and Y.L.; software, T.Z. and Y.L.; validation, H.Z. and B.W.; formal analysis, T.Z.; investigation, H.Z. and B.W.; resources, W.S.; data curation, Y.L.; writing—original draft preparation, T.Z. and Y.L.; writing—review and editing, H.S., F.X. and W.S.; visualization, P.X.; supervision, W.S.; funding acquisition, W.S. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the Special Project on Science and Technology Basic Resources Investigation, Investigation and Utilization of Wild Elite and Specific Germplasm Resources of *Cornus officinalis* in Eastern China (grant no. 2024FY100504-2).

**Data Availability Statement:** The data presented in this study are available in the Supplementary Materials, including the spatially filtered occurrence records, the accessible calibration-area boundary (M), and selected MaxEnt output tables. The occurrence and environmental data used in this study were derived from publicly available resources, including the Global Biodiversity Information Facility (GBIF; <https://doi.org/10.15468/dl.dbqz6t>), the National Specimen Information Infrastructure of China (NSII; <https://www.nsii.org.cn/2017/home-en.php>), the Chinese Virtual Herbarium (CVH; <https://www.cvh.ac.cn/>), Flora of China, WorldClim v2.1, CMIP6 datasets for ACCESS-CM2, BCC-

CSM2-MR, and CMCC-ESM2, NOAA-NCEI, and the Resource and Environmental Science Data Center, Chinese Academy of Sciences, as described in the Materials and Methods. Additional occurrence information was obtained from field surveys. Complete model settings and threshold calculations are reported in the Materials and Methods. Additional processed spatial layers and complete MaxEnt outputs generated in this study are available from the corresponding author upon reasonable request because of their large file sizes and the large number of intermediate raster products generated for the paleoclimatic, current, and future climate scenarios.

**Acknowledgments:** The authors thank the data providers and curators of GBIF, NSII, CVH, WorldClim, CMIP6, NOAA-NCEI, and the Resource and Environmental Science Data Center, Chinese Academy of Sciences, for access to biodiversity and environmental datasets.

**Conflicts of Interest:** Author Bin Wang was employed by the company Longshan Forest Farm. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## References

1. Zhao, Y.; Li, T.; Ma, C.; Liu, Z. Research Progress on Extraction, Health Benefits and Application of Active Components from the Medicinal and Edible Plant *Cornus Officinalis*. *Food Sci.* **2024**, *45*, 12–23. [\[CrossRef\]](#)
2. Deng, W.; Liu, Y.; Guo, Y.; Chen, J.; Abdu, H.I.; Khan, M.R.U.; Palanisamy, C.P.; Pei, J.; Abd El-Aty, A.M. A Comprehensive Review of *Cornus Officinalis*: Health Benefits, Phytochemistry, and Pharmacological Effects for Functional Drug and Food Development. *Front. Nutr.* **2024**, *10*, 1309963. [\[CrossRef\]](#) [\[PubMed\]](#)
3. Gao, X.; Liu, Y.; An, Z.; Ni, J. Active Components and Pharmacological Effects of *Cornus Officinalis*: Literature Review. *Front. Pharmacol.* **2021**, *12*, 633447. [\[CrossRef\]](#) [\[PubMed\]](#)
4. Zhang, N.; Yang, L.; Ma, Y.; Huang, J.; Zhu, S.; Dong, H.; Zhao, Z.; Lu, Y. Morphological, Chemical and Genetic Analyses Reveal High Diversity and Blurred Genetic Boundaries in *Cornus Officinalis* Siebold & Zucc. in China. *Ind. Crops Prod.* **2024**, *209*, 117941. [\[CrossRef\]](#)
5. Cao, B.; Bai, C.; Zhang, L.; Li, G.; Mao, M. Modeling Habitat Distribution of *Cornus Officinalis* with Maxent Modeling and Fuzzy Logics in China. *J. Plant Ecol.* **2016**, *9*, 742–751. [\[CrossRef\]](#)
6. Tulowiecki, S.J.; LaDuke, N. Models Reveal Shifting Distribution of Climatic Suitability for Pawpaw (*Asimina triloba* [L.] Dunal) Cultivation under Future Climate Change Scenarios. *Sci. Hortic.* **2024**, *338*, 113837. [\[CrossRef\]](#)
7. Feng, L.; Wang, H.; Ma, X.; Peng, H.; Shan, J. Modeling the Current Land Suitability and Future Dynamics of Global Soybean Cultivation under Climate Change Scenarios. *Field Crops Res.* **2021**, *263*, 108069. [\[CrossRef\]](#)
8. Hosseini, N.; Ghorbanpour, M.; Mostafavi, H. The Influence of Climate Change on the Future Distribution of Two *Thymus* Species in Iran: MaxEnt Model-Based Prediction. *BMC Plant Biol.* **2024**, *24*, 269. [\[CrossRef\]](#) [\[PubMed\]](#)
9. Erlichman, A.; Sandell, L.; Otto, S.P.; Aitken, S.N.; Ronce, O. Planting Long-lived Trees in a Warming Climate: Theory Shows the Importance of Stage-dependent Climatic Tolerance. *Evol. Appl.* **2024**, *17*, e13711. [\[CrossRef\]](#) [\[PubMed\]](#)
10. Lobell, D.B.; Field, C.B.; Cahill, K.N.; Bonfils, C. Impacts of Future Climate Change on California Perennial Crop Yields: Model Projections with Climate and Crop Uncertainties. *Agric. For. Meteorol.* **2006**, *141*, 208–218. [\[CrossRef\]](#)
11. Li, Y.; Li, M.; Li, C.; Liu, Z. Optimized Maxent Model Predictions of Climate Change Impacts on the Suitable Distribution of *Cunninghamia Lanceolata* in China. *Forests* **2020**, *11*, 302. [\[CrossRef\]](#)
12. Li, Y.; Shao, W.; Jiang, J. Predicting the Potential Global Distribution of *Sapindus Mukorossi* under Climate Change Based on MaxEnt Modelling. *Environ. Sci. Pollut. Res.* **2022**, *29*, 21751–21768. [\[CrossRef\]](#) [\[PubMed\]](#)
13. Ali, S.; Makanda, T.A.; Umair, M.; Ni, J. MaxEnt Model Strategies to Studying Current and Future Potential Land Suitability Dynamics of Wheat, Soybean and Rice Cultivation under Climatic Change Scenarios in East Asia. *PLoS ONE* **2023**, *18*, e0296182. [\[CrossRef\]](#) [\[PubMed\]](#)
14. Elith, J.; Phillips, S.J.; Hastie, T.; Dudík, M.; Chee, Y.E.; Yates, C.J. A Statistical Explanation of MaxEnt for Ecologists: Statistical Explanation of MaxEnt. *Divers. Distrib.* **2011**, *17*, 43–57. [\[CrossRef\]](#)
15. Zhao, N. *Cornus Germplasm Resources Evaluation by Molecular Markers and New Cultivars Selection*. Ph.D. Thesis, Henan Agricultural University, Zhengzhou, China, 2017.
16. Park, E.; Lee, C.G.; Kim, J.; Lim, E.; Hwang, S.; Yun, S.H.; Yong, Y.; Jeong, H.; Kim, J.A.; Jin, H.-S.; et al. Anti-Osteoporotic Effects of the Herbal Mixture of *Cornus Officinalis* and *Achyranthes Japonica* In Vitro and In Vivo. *Plants* **2020**, *9*, 1114. [\[CrossRef\]](#) [\[PubMed\]](#)
17. Sung, Y.-Y.; Kim, D.-S.; Kim, S.-H.; Yuk, H.J. Antihyperuricemic Effects of *Cornus Officinalis* Extract via URAT1 Regulation and Renoprotective Mechanisms. *Int. J. Mol. Sci.* **2025**, *26*, 9980. [\[CrossRef\]](#) [\[PubMed\]](#)

18. Huang, J.; Zhang, Y.; Dong, L.; Gao, Q.; Yin, L.; Quan, H.; Chen, R.; Fu, X.; Lin, D. Ethnopharmacology, Phytochemistry, and Pharmacology of *Cornus Officinalis* Sieb. et Zucc. *J. Ethnopharmacol.* **2018**, *213*, 280–301. [\[CrossRef\]](#) [\[PubMed\]](#)
19. Li, Y.; Shao, W.; Huang, S.; Zhang, Y.; Fang, H.; Jiang, J. Prediction of Suitable Habitats for *Sapindus Delavayi* Based on the MaxEnt Model. *Forests* **2022**, *13*, 1611. [\[CrossRef\]](#)
20. Syfert, M.M.; Smith, M.J.; Coomes, D.A. The Effects of Sampling Bias and Model Complexity on the Predictive Performance of MaxEnt Species Distribution Models. *PLoS ONE* **2013**, *8*, e55158. [\[CrossRef\]](#) [\[PubMed\]](#)
21. Otto-Bliesner, B.L.; Marshall, S.J.; Overpeck, J.T.; Miller, G.H.; Hu, A.; CAPE Last Interglacial Project Members. Simulating Arctic Climate Warmth and Icefield Retreat in the Last Interglaciation. *Science* **2006**, *311*, 1751–1753. [\[CrossRef\]](#) [\[PubMed\]](#)
22. Fick, S.E.; Hijmans, R.J. WorldClim 2: New 1-km Spatial Resolution Climate Surfaces for Global Land Areas. *Int. J. Climatol.* **2017**, *37*, 4302–4315. [\[CrossRef\]](#)
23. Eyring, V.; Bony, S.; Meehl, G.A.; Senior, C.A.; Stevens, B.; Stouffer, R.J.; Taylor, K.E. Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) Experimental Design and Organization. *Geosci. Model Dev.* **2016**, *9*, 1937–1958. [\[CrossRef\]](#)
24. Hijmans, R.J.; Cameron, S.E.; Parra, J.L.; Jones, P.G.; Jarvis, A. Very High Resolution Interpolated Climate Surfaces for Global Land Areas. *Int. J. Climatol.* **2005**, *25*, 1965–1978. [\[CrossRef\]](#)
25. Barve, N.; Barve, V.; Jiménez-Valverde, A.; Lira-Noriega, A.; Maher, S.P.; Peterson, A.T.; Soberón, J.; Villalobos, F. The Crucial Role of the Accessible Area in Ecological Niche Modeling and Species Distribution Modeling. *Ecol. Model.* **2011**, *222*, 1810–1819. [\[CrossRef\]](#)
26. Graham, M.H. Confronting multicollinearity in ecological multiple regression. *Ecology* **2003**, *84*, 2809–2815. [\[CrossRef\]](#)
27. Kass, J.M.; Muscarella, R.; Galante, P.J.; Bohl, C.L.; Pinilla-Buitrago, G.E.; Boria, R.A.; Soley-Guardia, M.; Anderson, R.P. ENMeval 2.0: Redesigned for Customizable and Reproducible Modeling of Species' Niches and Distributions. *Methods Ecol. Evol.* **2021**, *12*, 1602–1608. [\[CrossRef\]](#)
28. Roberts, D.R.; Bahn, V.; Ciuti, S.; Boyce, M.S.; Elith, J.; Guillera-Aroita, G.; Hauenstein, S.; Lahoz-Monfort, J.J.; Schröder, B.; Thuiller, W.; et al. Cross-validation Strategies for Data with Temporal, Spatial, Hierarchical, or Phylogenetic Structure. *Ecography* **2017**, *40*, 913–929. [\[CrossRef\]](#)
29. Valavi, R.; Elith, J.; Lahoz-Monfort, J.J.; Guillera-Aroita, G. BlockCV: An R Package for Generating Spatially or Environmentally Separated Folds for k-Fold Cross-Validation of Species Distribution Models. *Methods Ecol. Evol.* **2019**, *10*, 225–232. [\[CrossRef\]](#)
30. Hirzel, A.H.; Le Lay, G.; Helfer, V.; Randin, C.; Guisan, A. Evaluating the Ability of Habitat Suitability Models to Predict Species Presences. *Ecol. Model.* **2006**, *199*, 142–152. [\[CrossRef\]](#)
31. Phillips, S.J.; Anderson, R.P.; Dudík, M.; Schapire, R.E.; Blair, M.E. Opening the Black Box: An Open-source Release of Maxent. *Ecography* **2017**, *40*, 887–893. [\[CrossRef\]](#)
32. Merow, C.; Smith, M.J.; Silander, J.A. A Practical Guide to MaxEnt for Modeling Species' Distributions: What It Does, and Why Inputs and Settings Matter. *Ecography* **2013**, *36*, 1058–1069. [\[CrossRef\]](#)
33. Liu, C.; White, M.; Newell, G. Selecting Thresholds for the Prediction of Species Occurrence with Presence-only Data. *J. Biogeogr.* **2013**, *40*, 778–789. [\[CrossRef\]](#)
34. O'Neill, B.C.; Tebaldi, C.; Van Vuuren, D.P.; Eyring, V.; Friedlingstein, P.; Hurtt, G.; Knutti, R.; Kriegler, E.; Lamarque, J.-F.; Lowe, J.; et al. The Scenario Model Intercomparison Project (ScenarioMIP) for CMIP6. *Geosci. Model Dev.* **2016**, *9*, 3461–3482. [\[CrossRef\]](#)
35. Araujo, M.; New, M. Ensemble Forecasting of Species Distributions. *Trends Ecol. Evol.* **2007**, *22*, 42–47. [\[CrossRef\]](#) [\[PubMed\]](#)
36. Goberville, E.; Beaugrand, G.; Hautekèete, N.; Piquot, Y.; Luczak, C. Uncertainties in the Projection of Species Distributions Related to General Circulation Models. *Ecol. Evol.* **2015**, *5*, 1100–1116. [\[CrossRef\]](#) [\[PubMed\]](#)
37. Warren, D.L.; Seifert, S.N. Ecological Niche Modeling in Maxent: The Importance of Model Complexity and the Performance of Model Selection Criteria. *Ecol. Appl.* **2011**, *21*, 335–342. [\[CrossRef\]](#) [\[PubMed\]](#)
38. Radosavljevic, A.; Anderson, R.P. Making Better MAXENT Models of Species Distributions: Complexity, Overfitting and Evaluation. *J. Biogeogr.* **2014**, *41*, 629–643. [\[CrossRef\]](#)
39. Sakai, A.; Larcher, W. *Frost Survival of Plants*; Ecological Studies; Springer: Berlin/Heidelberg, Germany, 1987; Volume 62.
40. Körner, C.; Basler, D.; Hoch, G.; Kollas, C.; Lenz, A.; Randin, C.F.; Vitasse, Y.; Zimmermann, N.E. Where, Why and How? Explaining the Low-temperature Range Limits of Temperate Tree Species. *J. Ecol.* **2016**, *104*, 1076–1088. [\[CrossRef\]](#)
41. Choat, B.; Brodribb, T.J.; Brodersen, C.R.; Duursma, R.A.; López, R.; Medlyn, B.E. Triggers of Tree Mortality under Drought. *Nature* **2018**, *558*, 531–539. [\[CrossRef\]](#) [\[PubMed\]](#)
42. Harvey, J.E.; Smiljanić, M.; Scharnweber, T.; Buras, A.; Cedro, A.; Cruz-García, R.; Drobyshev, I.; Janecka, K.; Jansons, Ā.; Kaczka, R.; et al. Tree Growth Influenced by Warming Winter Climate and Summer Moisture Availability in Northern Temperate Forests. *Glob. Change Biol.* **2020**, *26*, 2505–2518. [\[CrossRef\]](#) [\[PubMed\]](#)
43. Corlett, R.T.; Westcott, D.A. Will Plant Movements Keep up with Climate Change? *Trends Ecol. Evol.* **2013**, *28*, 482–488. [\[CrossRef\]](#) [\[PubMed\]](#)

44. Murphy, P.C.; Knowles, J.F.; Moore, D.J.P.; Anchukaitis, K.; Potts, D.L.; Barron-Gafford, G.A. Topography Influences Species-Specific Patterns of Seasonal Primary Productivity in a Semiarid Montane Forest. *Tree Physiol.* **2020**, *40*, 1343–1354. [[CrossRef](#)] [[PubMed](#)]
45. Franklin, J. Species Distribution Modelling Supports the Study of Past, Present and Future Biogeographies. *J. Biogeogr.* **2023**, *50*, 1533–1545. [[CrossRef](#)]
46. Jiang, D.; Lang, X. Last Glacial Maximum East Asian Monsoon: Results of PMIP Simulations. *J. Clim.* **2010**, *23*, 5030–5038. [[CrossRef](#)]
47. Wu, J.; Liu, Q.; Wang, L.; Chu, G.; Liu, J. Vegetation and Climate Change during the Last Deglaciation in the Great Khingan Mountain, Northeastern China. *PLoS ONE* **2016**, *11*, e0146261. [[CrossRef](#)] [[PubMed](#)]
48. Tang, C.Q.; Matsui, T.; Ohashi, H.; Dong, Y.-F.; Momohara, A.; Herrando-Moraira, S.; Qian, S.; Yang, Y.; Ohsawa, M.; Luu, H.T.; et al. Identifying Long-Term Stable Refugia for Relict Plant Species in East Asia. *Nat. Commun.* **2018**, *9*, 4488. [[CrossRef](#)] [[PubMed](#)]
49. Gavin, D.G.; Fitzpatrick, M.C.; Gugger, P.F.; Heath, K.D.; Rodríguez-Sánchez, F.; Dobrowski, S.Z.; Hampe, A.; Hu, F.S.; Ashcroft, M.B.; Bartlein, P.J.; et al. Climate Refugia: Joint Inference from Fossil Records, Species Distribution Models and Phylogeography. *New Phytol.* **2014**, *204*, 37–54. [[CrossRef](#)] [[PubMed](#)]
50. Buisson, L.; Thuiller, W.; Casajus, N.; Lek, S.; Grenouillet, G. Uncertainty in Ensemble Forecasting of Species Distribution. *Glob. Change Biol.* **2010**, *16*, 1145–1157. [[CrossRef](#)]
51. Fordham, D.A.; Wigley, T.M.L.; Brook, B.W. Multi-Model Climate Projections for Biodiversity Risk Assessments. *Ecol. Appl.* **2011**, *21*, 3317–3331. [[CrossRef](#)]
52. Parmesan, C.; Yohe, G. A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems. *Nature* **2003**, *421*, 37–42. [[CrossRef](#)] [[PubMed](#)]
53. Lenoir, J.; Svenning, J.-C. Climate-related Range Shifts—A Global Multidimensional Synthesis and New Research Directions. *Ecography* **2015**, *38*, 15–28. [[CrossRef](#)]
54. Hewitt, N.; Klenk, N.; Smith, A.L.; Bazely, D.R.; Yan, N.; Wood, S.; MacLellan, J.I.; Lipsig-Mumme, C.; Henriques, I. Taking Stock of the Assisted Migration Debate. *Biol. Conserv.* **2011**, *144*, 2560–2572. [[CrossRef](#)]
55. Franklin, J. Species Distribution Models in Conservation Biogeography: Developments and Challenges. *Divers. Distrib.* **2013**, *19*, 1217–1223. [[CrossRef](#)]
56. Sofaer, H.R.; Jarnevich, C.S.; Flather, C.H. Misleading Prioritizations from Modelling Range Shifts under Climate Change. *Glob. Ecol. Biogeogr.* **2018**, *27*, 658–666. [[CrossRef](#)]
57. Draper, D.; Marques, I.; Iriondo, J.M. Species Distribution Models with Field Validation, a Key Approach for Successful Selection of Receptor Sites in Conservation Translocations. *Glob. Ecol. Conserv.* **2019**, *19*, e00653. [[CrossRef](#)]
58. Hållfors, M.H.; Liao, J.; Dzurisin, J.; Grundel, R.; Hyvärinen, M.; Towle, K.; Wu, G.C.; Hellmann, J.J. Addressing Potential Local Adaptation in Species Distribution Models: Implications for Conservation under Climate Change. *Ecol. Appl.* **2016**, *26*, 1154–1169. [[CrossRef](#)] [[PubMed](#)]
59. Piirainen, S.; Lehtikoinen, A.; Husby, M.; Kålås, J.A.; Lindström, Å.; Ovaskainen, O. Species Distributions Models May Predict Accurately Future Distributions but Poorly How Distributions Change: A Critical Perspective on Model Validation. *Divers. Distrib.* **2023**, *29*, 654–665. [[CrossRef](#)]

**Disclaimer/Publisher’s Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.