

Article

Predicting Habitat Suitability and Adaptation Strategies of an Endangered Endemic Species, *Camellia luteoflora* Li ex Chang (Ericales: Theaceae) under Future Climate Change

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Abstract: *Camellia luteoflora* Li ex Chang is an endangered plant endemic to the East Asian flora with high ornamental value as well as phylogenetic and floristic research value. Predicting the impact of climate change on its distribution and suitable habitat is crucial until scientific conservation measures are implemented. Based on seven environmental variables and 17 occurrence records, this study optimized the MaxEnt model using the kuenm data package to obtain the optimal parameter combinations (RM = 1.3, FC = LPT) and predicted the potential distribution pattern of *C. luteoflora* in various future periods. The results revealed that the mean diurnal range, temperature annual range, and precipitation of the wettest month were the influential factors determining the distribution pattern of *C. luteoflora*, contributing 60.2%, 14.4%, and 12.3% of the variability in the data, respectively. Under the current conditions, the area of suitable habitats for *C. luteoflora* was only about 21.9×10^4 km². Overall, the suitable area around the *C. luteoflora* distribution points will shrink in a circular pattern in response to future global warming, but some potentially suitable distribution areas will expand and migrate to higher latitudes and the Hengduan Mountains region, representing a survival strategy for coping with climate change. It is hypothesized that the future climate refugia will be the highly suitable area and the Hengduan Mountains region. Furthermore, a retrospective validation method was employed to assess the reliability of the predictions and estimate the model's predictive performance in the future. This study proposes a survival strategy and adaptation measures for *C. luteoflora* in response to climate change, and the proposed measures can be generalized for application in conservation planning and restoration processes. We also recommend that future studies incorporate factors such as the anthropogenic disturbances and associated socio-economic activities related to *C. luteoflora* into the model and to further predict the distribution pattern for *C. luteoflora* in response to historical climatic changes, tracing the evolutionary history of its population.

Keywords: *Camellia luteoflora*; climate change; MaxEnt model; model optimization; potential distribution; adaptation strategy



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1. Introduction

With the development of human society, the climate is becoming increasingly warmer and the frequency of extreme weather is increasing [1]. Climate change will directly lead to the destruction of the original habitats of many species, strongly affecting the current and future distribution patterns of plants globally [2], decreasing the population size of some plants, and even leading to the extinction of some plant species [3,4]. Therefore, before conservation biologists implement conservation measures for endangered species, it is

critical to understand how species will respond to future climate change and predict their extinction risk [5].

Recently, species distribution models (SDMs) have been extensively applied to predict existing distribution patterns of species and to assess the impacts of climate change on the distribution of species [6,7]. Predicting habitat suitability and species adaptation strategies via SDMs to delineate core areas for species conservation and management not only helps conservation practitioners to develop conservation strategies for endangered species resources, but it also strengthens conservation efforts in a more targeted manner to effectively help avert local extinction so that threatened species can be rapidly conserved [8]. Among the various SDMs, the maximum entropy model (MaxEnt) has the advantage of good predictive performance, short running time, and high simulation accuracy. Moreover, the MaxEnt model can effectively simulate the potential distributions of rare species with narrow ranges even when there are few known species distribution points and presence-only data [9]. For example, it has been widely applied in the prediction of potential distribution areas and habitat suitability evaluation of narrowly distributed species such as *Ostrya rehderiana* Chun (Fagales: Betulaceae) and *Cinnamomum mairei* Lévl. (Ranales: Lauraceae) [2,6].

The East Asian flora is an important part of the plant diversity of the Northern Hemisphere, which also includes a large number of endemic genera, most of which are monotypic or oligotypic [10]. The Sino-Himalayan subregion is recognized as a vital center of diversification and distribution of temperate flora in East Asia and even in the Northern Hemisphere [11]. *Camellia luteoflora* Li ex Chang (Ericales: Theaceae) is endemic to the Sino-Himalayan subregion and was first discovered in Chishui, Guizhou in 1981 [12], with small, delicate, bright yellow flowers of high ornamental value [13]. From a phylogenetic point of view, *C. luteoflora* is one of the more primitive populations in the genus *Camellia* L. and has been hypothesized to be an ancient relict species [14], which is of high phylogenetic and floristic research value [15]. According to the preliminary survey, *C. luteoflora* is only distributed in Luzhou and Yibin, Sichuan Province, and Chishui, Guizhou Province, with an extremely narrow distribution and a small number of wild populations [13], coupled with human activity interference and animal hazards, such as road construction, reclamation of slopes, long-term logging, rodent infestation, etc., which shrunk the suitable habitat of *C. luteoflora* and the number of the population showed a decreasing trend. *C. luteoflora* is classified as “Critically Endangered” by the IUCN Red List of Threatened Species (<https://www.iucnredlist.org/species/62055668/62055674>, accessed on 20 September 2023). Currently, the research on *C. luteoflora* focuses on reproduction techniques, population structure, community ecology, genetic diversity [16] and phylogenetic relationships [15], physiological and biochemical characteristics, and the investigation of the causes of endangerment [17]. Based on the maximum entropy model, Dai et al. predicted the current potential distribution area of *C. luteoflora* and discussed the main environmental factors affecting its distribution [18]. However, this study only predicted and assessed the known existing distribution areas and neighboring areas of *C. luteoflora* and it could not guarantee a sufficient spatial scale and high accuracy at the same time. Moreover, due to increasing climate change in the future, current areas suitable for *C. luteoflora* may be unfavorable for *C. luteoflora* habitation in the future. Thus, it is hard to directly delimit suitable areas and restoration sites of *C. luteoflora* using existing occurrence records. To provide scientific guidance for the conservation of *C. luteoflora*, it is imperative to clarify how future climate change will affect the population dynamics of *C. luteoflora* under increasing climate change and how the distribution pattern of *C. luteoflora* populations will respond to future changes in environmental and climatic conditions.

Therefore, this study combined the Maxent model and ArcGIS spatial analysis techniques to predict the potential changes in the geographical distribution of *C. luteoflora* in China under different climatic conditions with the aim of investigating the following issues: (1) to more accurately predict the potential geographic distribution pattern of *C. luteoflora* under current climatic conditions based on the parameter settings of the optimal Maxent

model, taking into account the effects of bias and small sample sizes; (2) to explore the important environmental factors affecting the potential geographic distribution of *C. luteoflora*; and (3) to predict habitat suitability and adaptation strategies of *C. luteoflora* under future climate change scenarios.

This study proposes to predict the response of *C. luteoflora* to future changes in environmental and climatic conditions as a means to better understand its needs for growth environmental factors and its coping mechanisms to environmental changes. In addition, this study will provide a paradigm for studying the response of endangered species to future climate change, as well as a scientific rationale for more targeted conservation measures.

2. Materials and Methods

2.1. Species Data Collection

To ensure the completeness of the geographic distribution data of *C. luteoflora*, this study not only carried out field surveys and a literature review but also searched databases including Chinese Virtual Herbarium, Global Biodiversity Information Facility, Plant Photo Bank of China, National Specimen Information Infrastructure, and other electronic literature resources.

We deleted duplicated, incomplete, and artificially introduced records from the retrieved distribution data and added two newly discovered occurrence data via field surveys, resulting in a total of 22 known distribution points (Figure 1). To mitigate the potential effects of sampling bias and spatial autocorrelation, we retained one of the locations with a distance of less than 3 km between them and finally obtained 17 distribution points (Table S1).

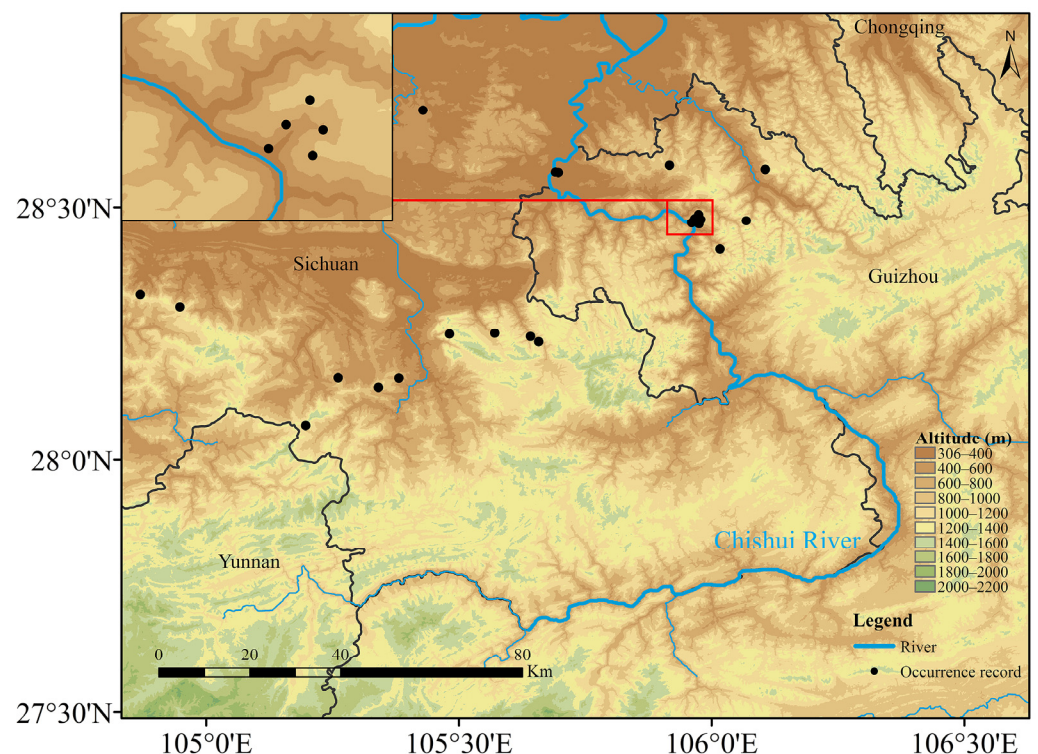


Figure 1. Distribution of *C. luteoflora* in China, with black dots representing the location of occurrence records for *C. luteoflora*.

2.2. Environmental Variables

A total of 22 environmental variables were selected for this study, including three topographic factors (altitude, slope, and aspect) and 19 bioclimatic variables. The 19 bioclimatic variables with a resolution of 2.5 arc minute were downloaded from the Worldclim

database [19] for the current (1970–2000) and future (2030s, 2021–2040; 2050s, 2041–2060; 2070s, 2061–2080; and 2090s, 2081–2100). For the future four periods of climate data, according to the Coupled Model Intercomparison Project Phase 6 (CMIP6) [20], the data under four different shared socioeconomic pathways were downloaded via CNRM-ESM2-1 [21], i.e., SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5, which represent approximate global effective radiative forcing values stabilized at 2.6 W/m², 4.5 W/m², 7.0 W/m², and 8.5 W/m² at the end of the year 2100, respectively [22–24].

In order to reduce the adverse effects of multicollinearity among environmental variables on modeling [25,26], the contribution rates of 22 environmental variables were calculated by importing the distribution data and environmental data into MaxEnt and removing the environmental variables whose contribution rates were 0, and the Pearson correlation coefficient (r) between environmental variables was calculated using ENMTools.pl software (<https://github.com/danlwarren/ENMTools>, accessed on 20 September 2023) [27]. For variables with $r \geq 0.8$, the higher contributing variables were retained. After these two processes, seven environmental variables were finally selected for modeling (construction of species distribution models) [28] (Table 1).

Table 1. The environmental variables screened for this study and their relative proportions of contribution.

Variable	Description	Unit	Percent Contribution (%)
bio2	Mean diurnal range	°C	60.2
bio7	Temperature annual range	°C	14.4
bio13	Precipitation of wettest month	mm	12.3
bio15	Precipitation seasonality	%	5.2
bio19	Precipitation of coldest quarter	mm	3.5
Alt	Altitude	m	2.7
bio6	Minimum temperature of coldest month	°C	1.7

2.3. Model Parameters Tuning

Niche models based on fine-tuned Maxent settings typically showed better discrimination than the models with default settings [29]. In order to improve the predictive accuracy and reliability of the model, optimization was performed by invoking two important parameter (RM regularization multiplier, FC feature combination) settings used in MaxEnt to balance the goodness-of-fit and complexity of the model [30]. Model selection was based on statistical significance, predictive capability, and model complexity [31,32]. The Akaike information criterion (AIC) assesses the fitting and complexity of the model and is the standard for measuring the model performance [33], where the model with the lowest complexity ($\Delta AIC_c < 2$) was selected among the significant and low-omission (omission rate $< 5\%$) candidate models. Therefore, this study generated model predictions (29 feature classes \times 40 regularization multipliers = 1160 models) based on 17 current distribution points and seven environmental variables using the Kuenm package, calling MaxEnt for each combination of FC and RM (0.1–4, with an interval of 0.1) settings. Based on the Akaike information criterion correction (AIC_c), the most parsimonious and optimal model was selected to predict the potential geographic distribution of *C. luteoflora* in China.

However, the enhancement of MaxEnt performance within a single time period may not ensure transferability between time periods [34]. To validate the temporal transferability and predictive accuracy of the MaxEnt model, based on the distribution data for the periods 1970 to 2000 (“historical”) (Table S2) and 2021 to 2040 (“current”), MaxEnt predicted the current time period (the “future” time period associated with the model fitting data) using the historical data by comparing the predictions with the current data to assess the consistency of the predictions with the current known distribution of *C. luteoflora* [35].

2.4. MaxEnt Model

Species distributions were modeled using MaxEnt version 3.4.1, with 25% of the distribution points selected as the test set and the other 75% as the training set, and cross-validation was repeated for 10 runs. Response curves were plotted and the relative contribution of each environmental variable was assessed using the jackknife test [36]. A greater gain value with an individual variable indicates that more information or contribution towards species habitats distribution is contained in the variable [37]. The area under the ROC curve (AUC), calculated from the receiver operating characteristic (ROC) curve, was used as an indicator for evaluating the model performance [38]. The area under the curve is positively correlated with the performance of the predictive model [37].

The final output ASCII format file is the average of 10 repetitions, and the resultant file is imported into ArcGIS 10.8 software to be converted into a raster file and then mapped onto a map for visualization and reclassification. Referring to the Intergovernmental Panel on the Climate Change (IPCC) report and taking into account the actual situation of *C. luteoflora*, the habitat suitability was classified according to the probability of existence. The habitat suitability of *C. luteoflora* was divided as follows: ($p < 0.05$) unsuitable habitats, ($0.05 \leq p < 0.33$) low suitability habitats, ($0.33 \leq p < 0.66$) moderate suitability habitats, and ($p \geq 0.66$) high suitability habitats. Habitat suitability index (HSI) was also extracted for all the existing distribution points under different time periods in the current and future, and the suitability of the habitats for *C. luteoflora* was measured based on the assessment of habitat attributes.

2.5. Species Potential Distribution Changes and Centroid Shifts

The area of different suitable habitats under different periods was computed by applying ArcGIS 10.8 software. In order to further study the trend of changes in the area of suitable habitats, the python-based SDMtoolbox [39] was used to reclassify the current and future output raster files of *C. luteoflora* into a binary file format. Then, we selected “Distribution Changes Between Binary SDMs” and “Centroid Changes (Lines)” in the “SDM Tools” module to calculate and compare changes in the potential distribution areas and the centroid shifts under current and future climate scenarios, in addition to analyzing the overall migration trends and centroid tracks of *C. luteoflora* [40].

3. Results

3.1. Model Optimization and Evaluation

When RM is 1.3 and FC is LPT, delta AICc takes the value of 0, so this parameter combination was considered as the optimal combination [30,41] (Figure S1). Compared to the model with default settings, the value of delta AICc for the optimized settings decreased to 0, the value of AUC_{DIFF} (the difference between the training AUC and the test AUC) decreased to 0.0032, and the average AUC increased to 0.997 (Table 2). The results verified that the model had an extremely accurate prediction level, indicating that the optimized MaxEnt model reduced the overfitting degree and complexity and enhanced the accuracy of the prediction results.

Table 2. Optimization of model parameters for *C. luteoflora* and comparison of model performance under default and optimized settings.

Type	RM	FC	Mean AUC	AUC _{DIFF}	Delta AICc
Default	1	LQHPT	0.995	0.0051	28.31
Optimization	1.3	LPT	0.997	0.0032	0

3.2. Vital Environmental Factors Influencing the Distribution

By screening the contribution rates and the correlation coefficients among environmental variables (Figure 2), seven environmental variables were finally selected from 22 environmental variables to predict the potential distribution of *C. luteoflora*. The con-

tribution of each environmental variable to the suitable distribution area of *C. luteoflora* was calculated using the jackknife test and the three variables with the highest contribution were bio2 (60.2%), bio7 (14.4%), and bio13 (12.3%) (Table 1), with a cumulative contribution rate of 86.9%. When using only individual variables for model prediction, bio2 had the highest regularized training gain, test gain, and AUC values, followed by bio7 and bio13 (Figure 3). In summary, the mean diurnal range, temperature annual range, and precipitation of the wettest month have the largest impact on the growth suitability of *C. luteoflora* and are considered to be the main environmental constraints affecting the distribution of *C. luteoflora*. Based on the response curves of the main environmental variables (Figure 4), the suitability ranges of the seven main environmental variables for *C. luteoflora* could be obtained. The suitable mean diurnal range was from 5.33 to 6.83 °C, the suitable range for minimum temperature of the coldest month was from 0.92 to 5.55 °C, the suitable temperature annual range was from 25.08 to 27.25 °C, the suitable range for precipitation of the wettest month was from 161.42 to 195.75 mm, the suitable range for precipitation seasonality was from 64.36 to 72.99 mm, the suitable range for precipitation of the coldest quarter was from 50.03 to 66.56 mm, and the suitable altitude range was from 477 to 1242 m.

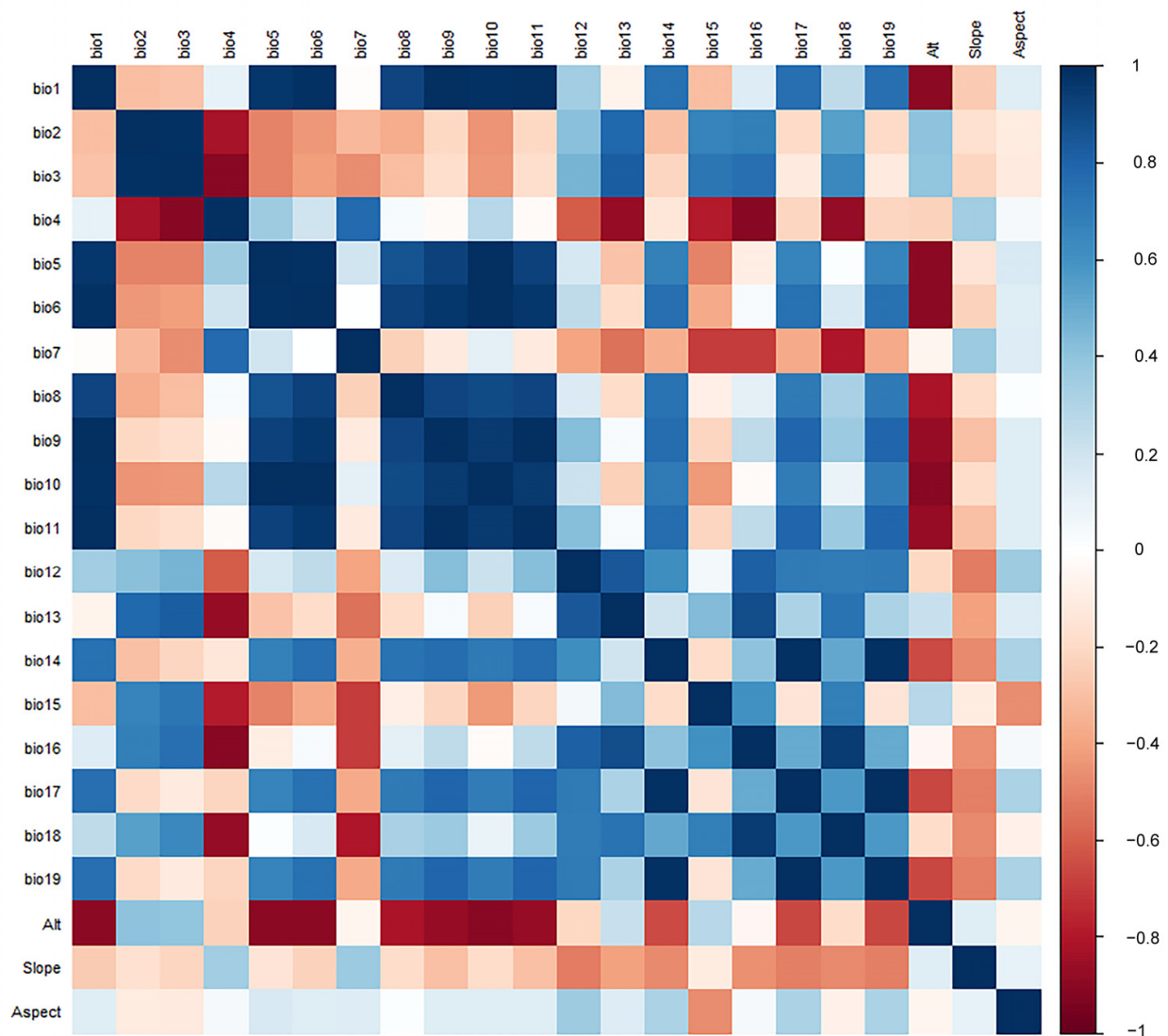


Figure 2. Portraying the Pearson's correlation of all environmental variables considered.

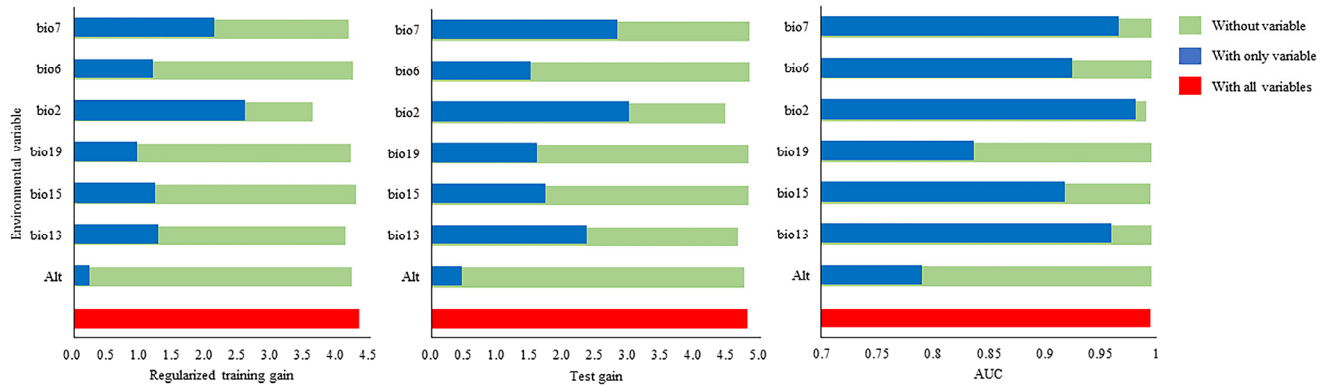


Figure 3. Jackknife plot of training gain for *C. luteoflora* indicating the influence of variables.

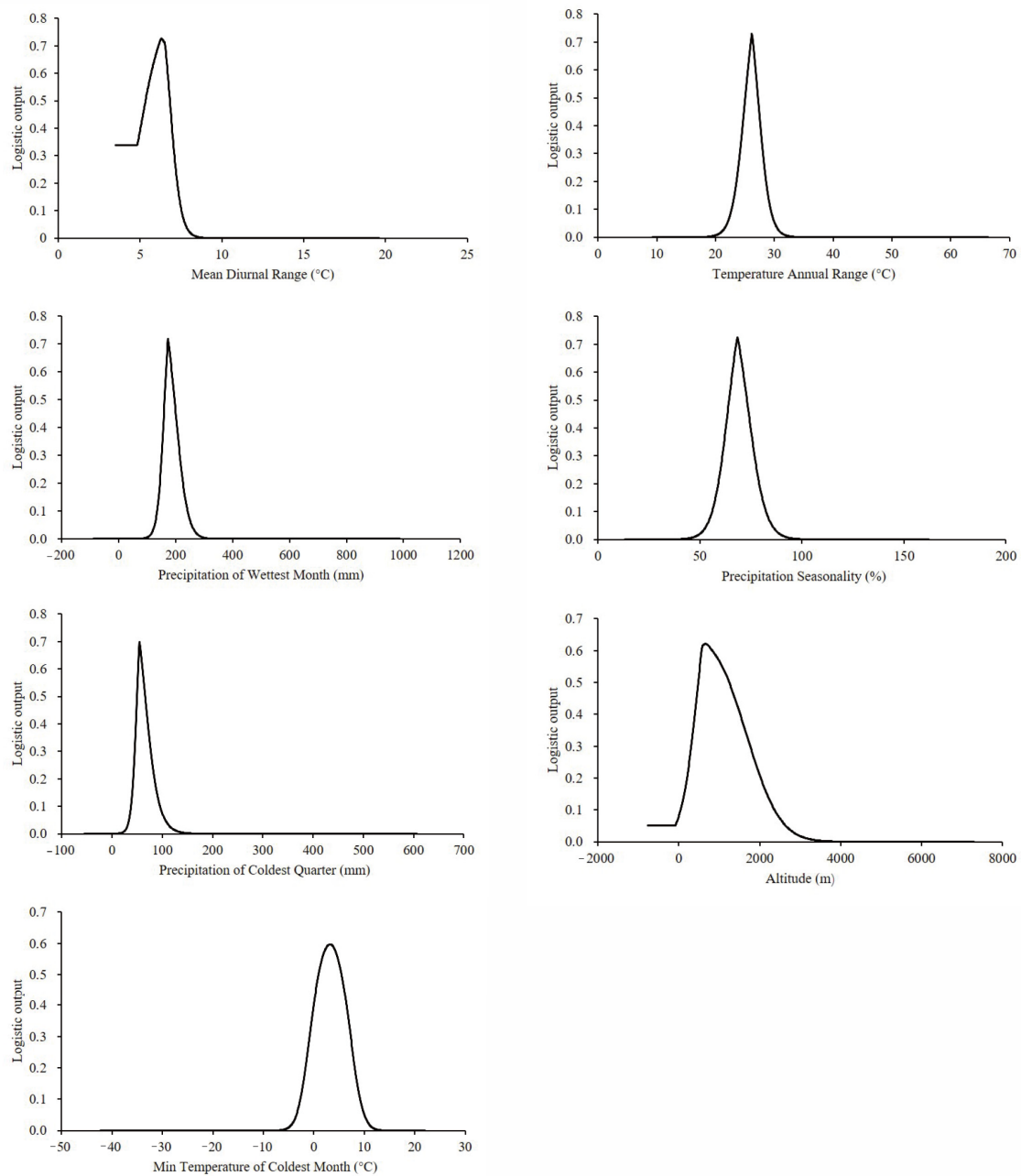


Figure 4. Response curves of significant environmental variables in the *C. luteoflora* distribution model.

3.3. Current Potential Distribution and Suitability

The potential distribution of *C. luteoflora* under the current conditions is shown in Figure 5. The potentially suitable distribution areas of *C. luteoflora* include Guizhou, Sichuan, Yunnan, Shaanxi, and Gansu provinces and Chongqing city. The high suitability area, covering $0.58 \times 10^4 \text{ km}^2$, was near the border between Sichuan and Guizhou. The moderately suitable area was about $2.24 \times 10^4 \text{ km}^2$, mainly located near the junction of Sichuan, Guizhou, and Chongqing, followed by a very small distribution in Yunnan. The lowly suitable area was mainly located in northwestern Guizhou, southeastern Sichuan, southwestern Chongqing, southern Shaanxi, and a few discontinuous distribution areas of Yunnan and Gansu, covering $19.08 \times 10^4 \text{ km}^2$. The highly, moderately, and lowly suitable areas accounted for 0.061%, 0.233%, and 1.987% of the study region, respectively (Table 3).

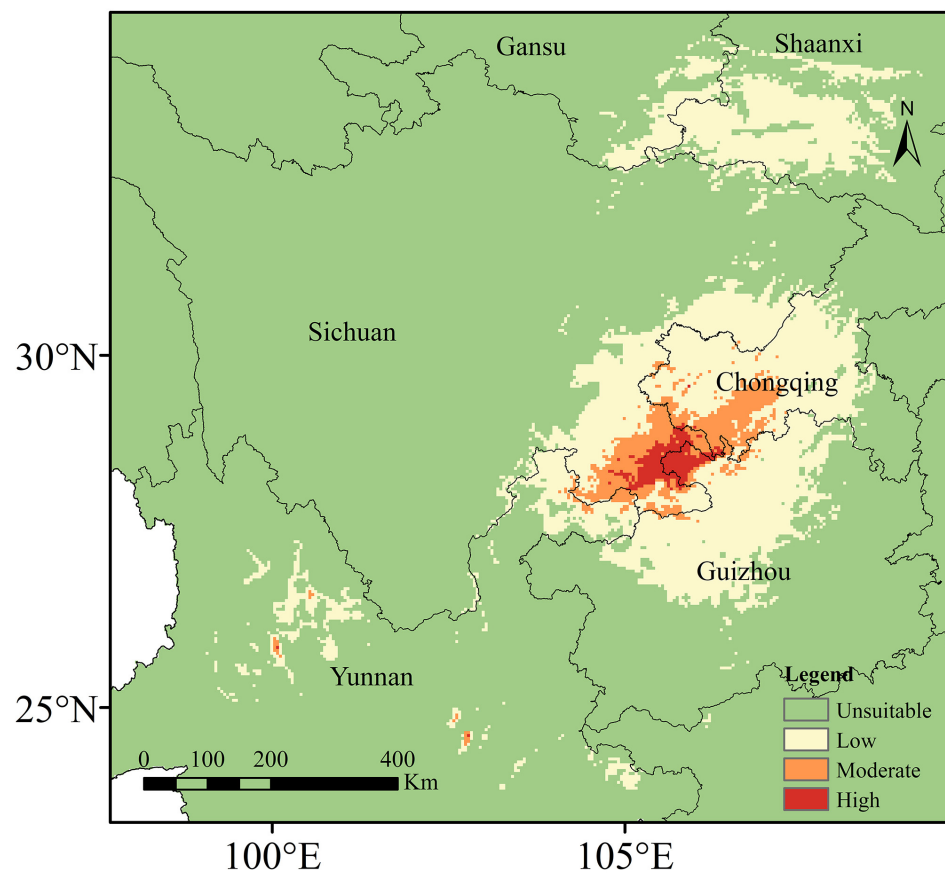


Figure 5. The suitable habitat for *C. luteoflora* under current climatic conditions.

3.4. Potentially Suitable Distribution under Future Climate Changes

Under future climate change scenarios, some regions that were currently unsuitable for *C. luteoflora* would become highly suitable, such as the Hengduan Mountains region, which would have highly suitable areas in 2081–2100 under the SSP5-8.5 scenario (Figure 6). The highly and moderately suitable habitats of *C. luteoflora* were still mainly concentrated in southeastern Sichuan, northwestern Guizhou, and southern Chongqing, and the area of highly and moderately suitable habitats under different scenarios and periods in the future would be reduced by $0.22 \times 10^4 \text{ km}^2$ to $0.57 \times 10^4 \text{ km}^2$ and $0.22 \times 10^4 \text{ km}^2$ to $1.93 \times 10^4 \text{ km}^2$, respectively. In particular, the area of highly and moderately suitable habitats under SSP1-2.6 (2090s), SSP2-4.5 (2090s), and SSP3-7.0 (2070s) would decrease significantly, from $0.58 \times 10^4 \text{ km}^2$ to $0.01 \times 10^4 \text{ km}^2$ and from $2.24 \times 10^4 \text{ km}^2$ to $0.31 \times 10^4 \text{ km}^2$, respectively (Table 3). The aggregate area of lowly suitable and unsuitable habitats would increase by $0.73 \times 10^4 \text{ km}^2$ to $2.49 \times 10^4 \text{ km}^2$ at different times in the future. The highly and moderately suitable habitats would shrink

a little as the climate warms, while the lowly suitable and unsuitable habitats would expand slightly.

Table 3. Projected areas of *C. luteoflora* habitat under current and future climate conditions.

Climate Scenarios	Time Period	Unsuitable Habitat		Lowly Suitable Habitat		Moderately Suitable Habitat		Highly Suitable Habitat	
		10 ⁴ km ²	%	10 ⁴ km ²	%	10 ⁴ km ²	%	10 ⁴ km ²	%
Current	1970–2000	938.10	97.719	19.08	1.987	2.24	0.233	0.58	0.061
SSP1–2.6	2021–2040	947.94	98.744	11.73	1.222	0.31	0.033	0.01	0.001
	2041–2060	941.37	98.059	17.43	1.816	1.13	0.117	0.07	0.008
	2061–2080	936.77	97.580	21.45	2.234	1.75	0.183	0.03	0.003
	2081–2100	942.29	98.156	16.99	1.770	0.66	0.069	0.05	0.006
SSP2–4.5	2021–2040	941.56	98.079	17.60	1.833	0.83	0.087	0.01	0.001
	2041–2060	943.22	98.252	15.89	1.655	0.88	0.091	0.01	0.001
	2061–2080	945.31	98.469	13.77	1.435	0.89	0.093	0.03	0.003
	2081–2100	942.49	98.176	17.09	1.780	0.40	0.042	0.01	0.001
SSP3–7.0	2021–2040	945.14	98.452	14.30	1.490	0.55	0.057	0.01	0.001
	2041–2060	935.11	97.407	22.80	2.375	2.02	0.210	0.08	0.008
	2061–2080	944.47	98.382	15.16	1.579	0.33	0.035	0.03	0.004
	2081–2100	939.16	97.829	20.05	2.088	0.72	0.074	0.07	0.008
SSP5–8.5	2021–2040	938.02	97.711	19.98	2.082	1.79	0.187	0.20	0.021
	2041–2060	945.95	98.536	13.18	1.373	0.86	0.089	0.02	0.002
	2061–2080	940.42	97.960	18.97	1.976	0.58	0.061	0.03	0.003
	2081–2100	940.72	97.991	17.84	1.858	1.08	0.112	0.36	0.038

Compared with the current potentially suitable habitats, the expansion of the suitable habitats area for *C. luteoflora* ranged from 1.56×10^4 km² to 10.96×10^4 km² (Table 4), with most of the increased suitable habitats occurring in the southwestern part of the original suitable habitats area; at the same time, the suitable habitats located in Gansu and Shaanxi would significantly shift northward (Figure 7). Under different future scenarios, the suitable habitats of *C. luteoflora* would migrate to central Yunnan and the Hengduan Mountains; especially, the expansion area under SSP3–7.0 (2050s, 2070s, and 2090s) and SSP5–8.5 (2070s and 2090s) had a significant increase in the Hengduan Mountains region. The contraction of suitable habitats area ranged from 4.01×10^4 km² to 13.2×10^4 km², mainly in southeastern Sichuan, northwestern Guizhou, northeastern Yunnan, central Chongqing, and southern Shaanxi. The range of stabilization of the suitable habitats area is from 8.68×10^4 km² to 17.87×10^4 km². The suitable habitats area concentrated in southeastern Sichuan, northeastern Yunnan, northwestern Guizhou, and southwestern Chongqing continued to shrink in a circular pattern under different future scenarios, and this contraction area formed a circular region around the stability region, which covered Sichuan, Chongqing, Guizhou, and Yunnan.

Habitat suitability index (HSI) is used to forecast the impacts of climate change on species and to indicate the potential risks to the suitability of existing sites in the future, which in turn facilitates the adoption of effective measures to protect existing sites in advance [42]. HSI would decline significantly from 2021–2040 under all scenarios. HSI under the SSP1–2.6 and SSP2–4.5 scenarios would follow a similar trend, decreasing and then increasing slightly before stabilizing from 2041–2060, while HSI under the SSP5–8.5 scenario would continue a downward trend (Figure 8). In general, HSI for distribution points 6, 7, 8, 12, and 21 would continue to be low while also being lower than the other distribution points.

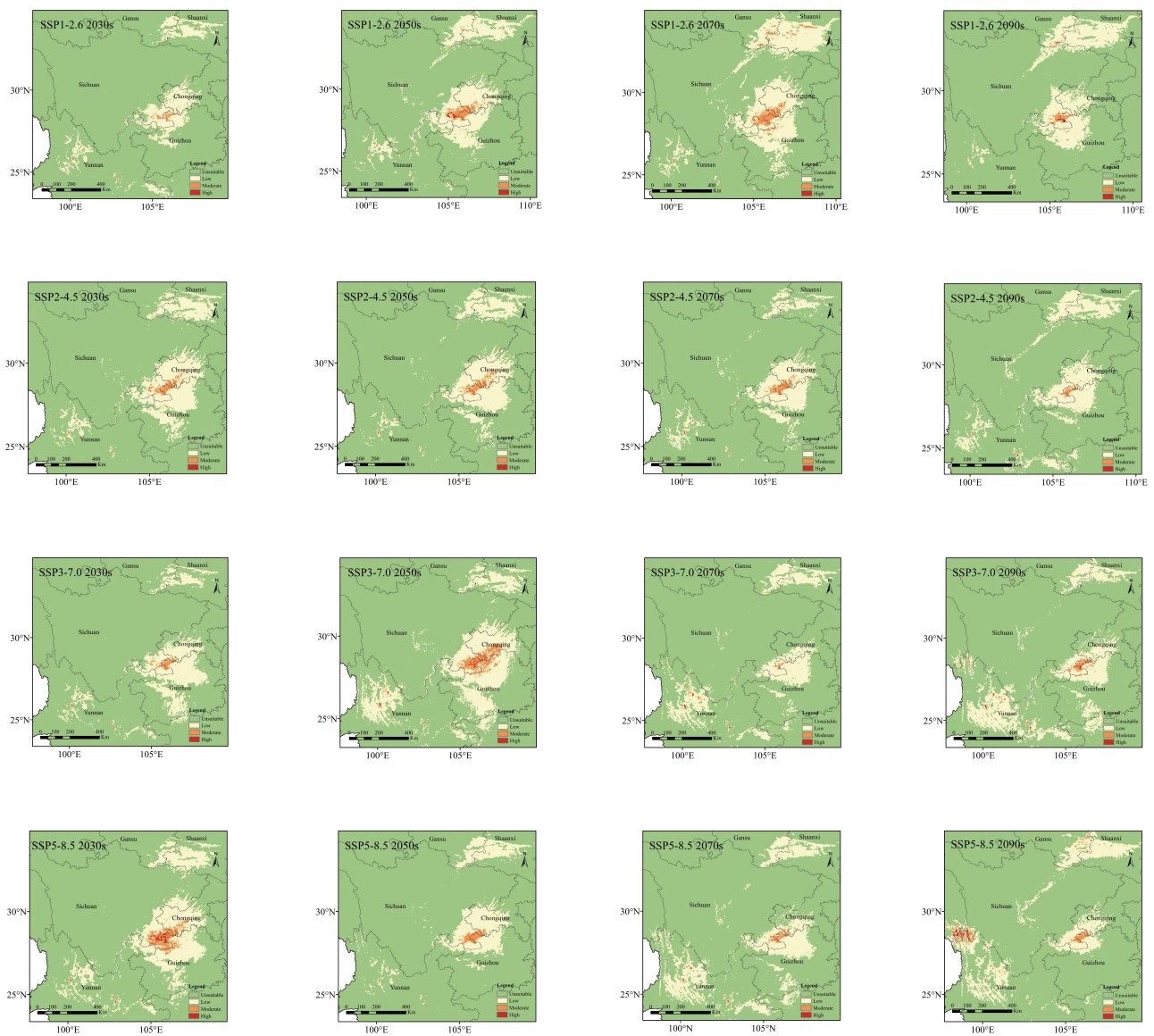


Figure 6. Projected potential distribution areas of *C. luteoflora* under different future climate scenarios.

Table 4. Area changes in the potential distribution of *C. luteoflora* under climate scenarios.

Scenarios	Time Period	Range Expansion 10 ⁴ km ²	Instability 10 ⁴ km ²	Stability 10 ⁴ km ²	Range Contraction 10 ⁴ km ²
SSP1-2.6	2021–2040	1.56	936.56	10.49	11.39
	2041–2060	3.49	934.63	15.14	6.75
	2061–2080	6.01	932.10	17.20	4.68
	2081–2100	3.63	934.49	14.07	7.81
SSP2-4.5	2021–2040	2.48	935.64	15.95	5.93
	2041–2060	1.81	936.31	14.96	6.92
	2061–2080	2.02	936.10	12.67	9.22
	2081–2100	4.94	933.17	12.55	9.33
SSP3-7.0	2021–2040	2.92	935.19	11.93	9.96
	2041–2060	8.42	929.70	16.46	5.43
	2061–2080	6.03	932.09	9.49	12.39
	2081–2100	10.96	927.16	9.87	12.01
SSP5-8.5	2021–2040	4.09	934.02	17.87	4.01
	2041–2060	1.79	936.33	12.26	9.62
	2061–2080	9.28	928.84	10.30	11.59
	2081–2100	10.59	927.52	8.68	13.20

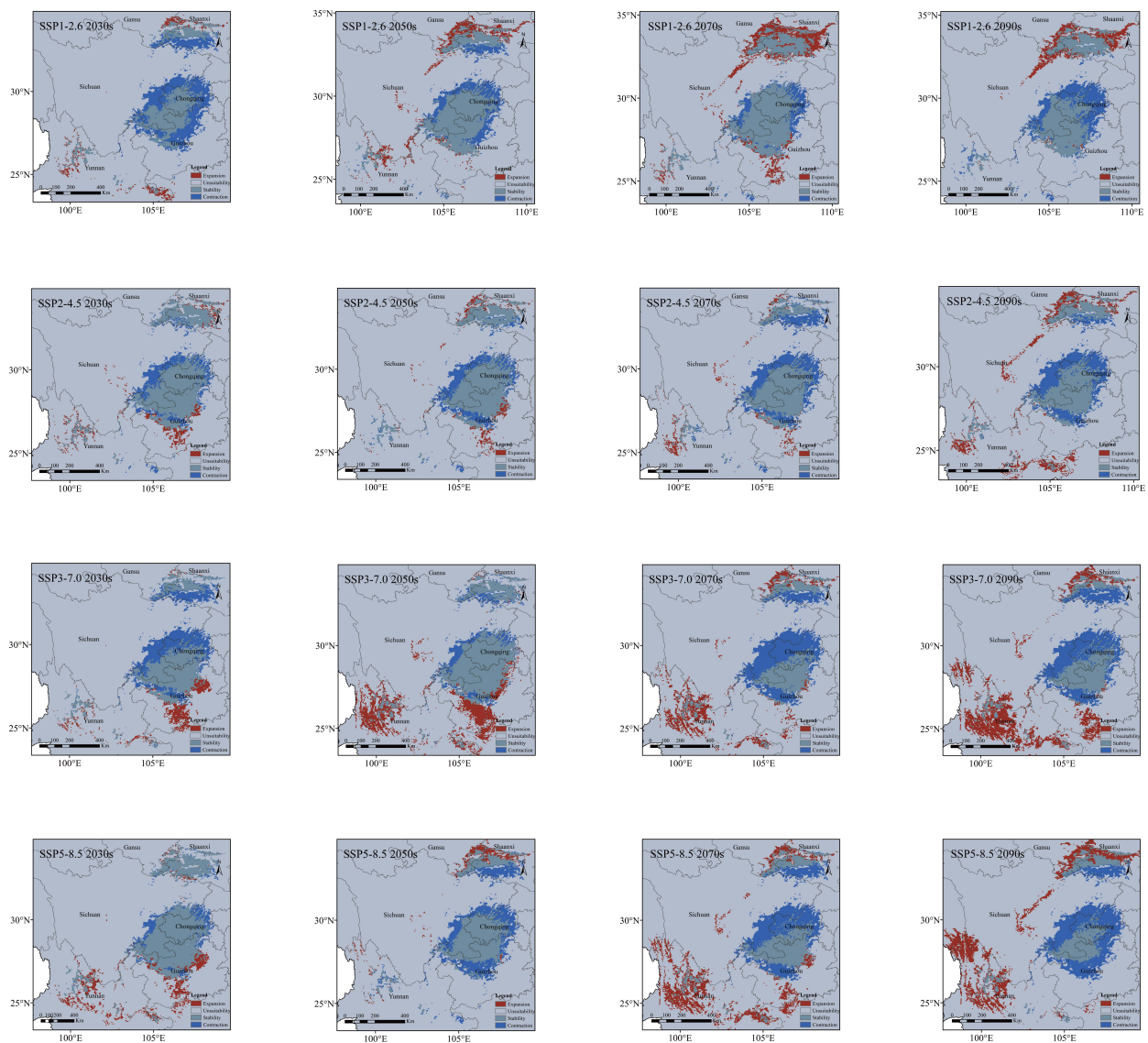


Figure 7. Changes in habitat suitability under future climate scenarios compared to current conditions.

3.5. Centroid Shifts of Suitable Habitats under Different Climatic Conditions

The centroid of the suitable area for *C. luteoflora* under the current climatic conditions was located at 29.191° N, 107.131° E, near the border between Chongqing Municipality and Guizhou Province (Figure 9A). Compared to the centroid under the current conditions, which was 47.58–390.44 km away from the centroids under future climate scenarios, the centroid of the suitable area for *C. luteoflora* would first move southwest and then to the north under the SSP1-2.6 scenario (Figure 9B). Under the other three future climate scenarios, the projected centroids would generally shift southwest, except for two centroids moving northwest (2041–2060 under the SSP2-4.5 and SSP5-5.8 scenarios). Overall, there would be a tendency for the centroids of *C. luteoflora* to migrate to higher latitudes and altitudes in the north and southwest.

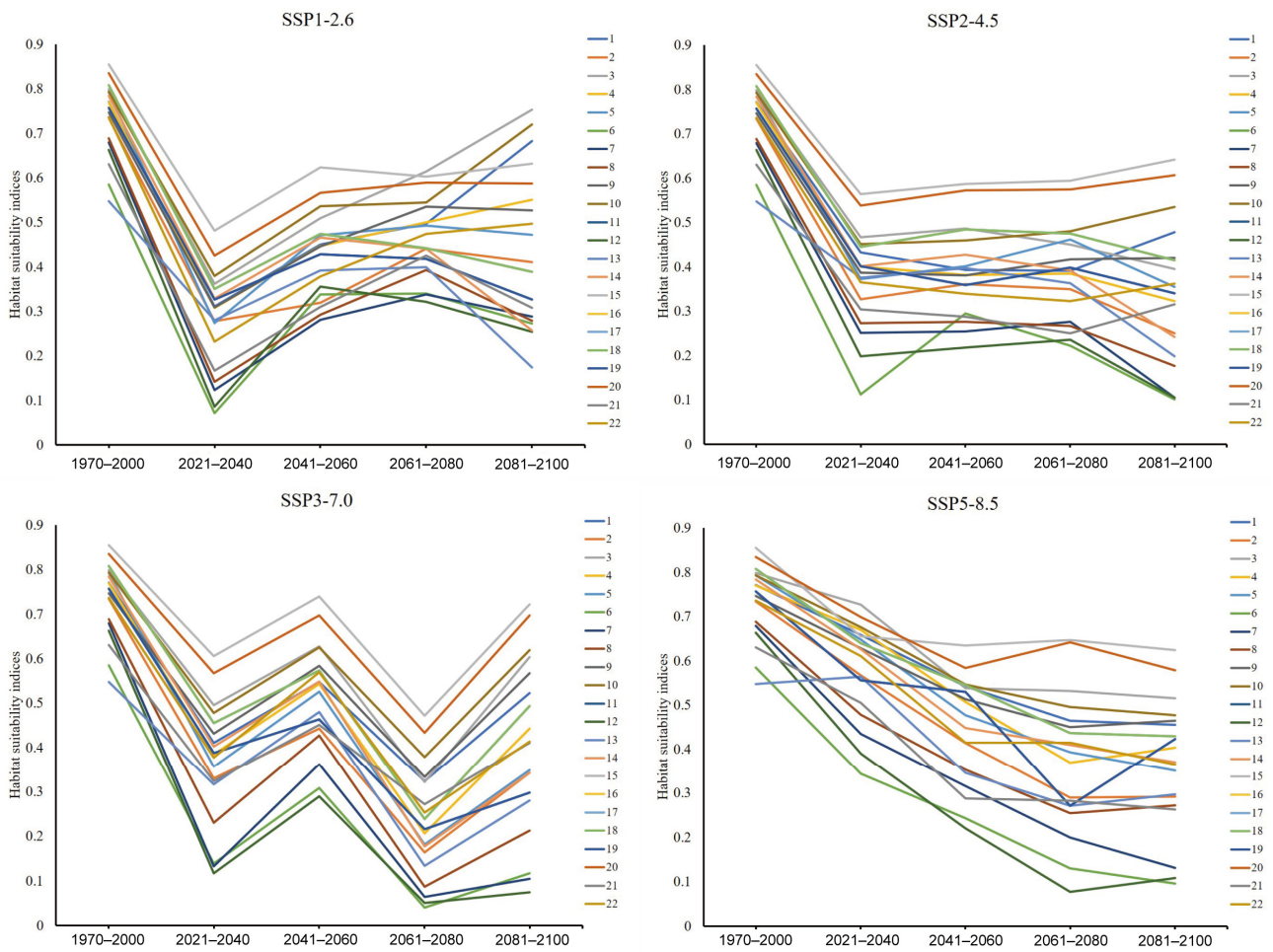


Figure 8. Changes in HSI at existing distribution points of *C. luteoflora* under future climate scenarios.

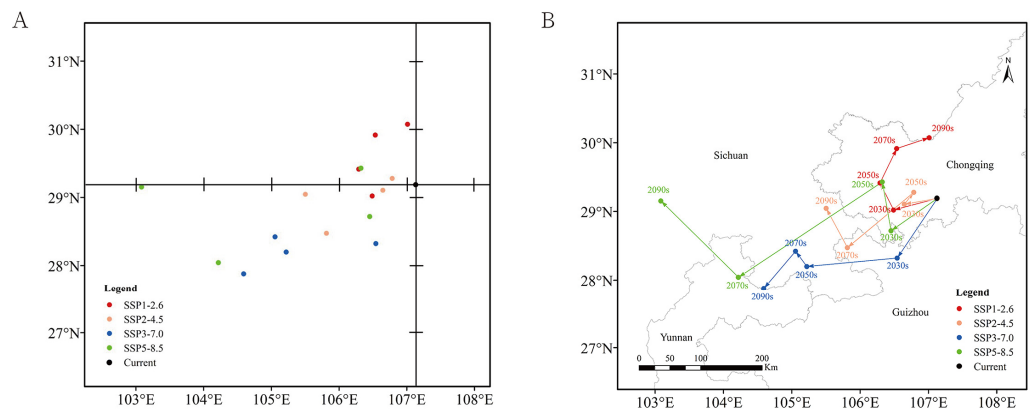


Figure 9. Shifts in the centroid of suitable habitats for *C. luteoflora* under current conditions and future climate scenarios.

4. Discussion

The model accuracy is affected not only by the type of environmental factors but also by the number of species distribution points [43]. Big sample sizes and simple prediction environmental factors will reduce the prediction accuracy, while small sample sizes will provide a conservative description of ecological niche [44]. However, datasets with sampling bias and small sample sizes are particularly prone to model overfitting when assessing the conservation status of endangered species, and therefore, the model ought to be adjusted in a more targeted manner [45]. This study referred to recent

studies of species-specific tuning of model parameter settings [30,46], which resulted in better model performance and prediction compared to using the default settings. When compared to previous studies by Dai et al. [18], this study considered the effects of bias and small sample size on the modeling of the distribution of *C. luteoflora*, adjusted the model parameter (RM and FC) settings for *C. luteoflora*, and predicted the potential distribution of *C. luteoflora* in China using the optimal MaxEnt model while ensuring sufficient spatial scales and high accuracy.

To further validate the accuracy of the MaxEnt model predictions with an example, MaxEnt was applied to predict the potential distribution of *C. luteoflora* under four climate scenarios in 2021–2040 (Figure 10), based on records from six distribution points at the site of the first discovery (Chishui) during the period from 1970 to 2000 (“historical”). A total of 22 existing distribution points were found until 2023 and all of them were distributed within suitable habitats under different climate scenarios in 2021–2040, where most of the extant points were distributed within highly and moderately suitable habitats, which to some extent verified that the optimized MaxEnt model had relatively high temporal transferability and accuracy. In addition, the predicted ranges of potentially suitable habitats of *C. luteoflora* for 2021–2040 were similar based on the six distribution points located in Chishui in 1970–2000 and based on the 17 existing distribution points in 1970–2000, respectively, thus further illustrating the reliability of the modeling results.

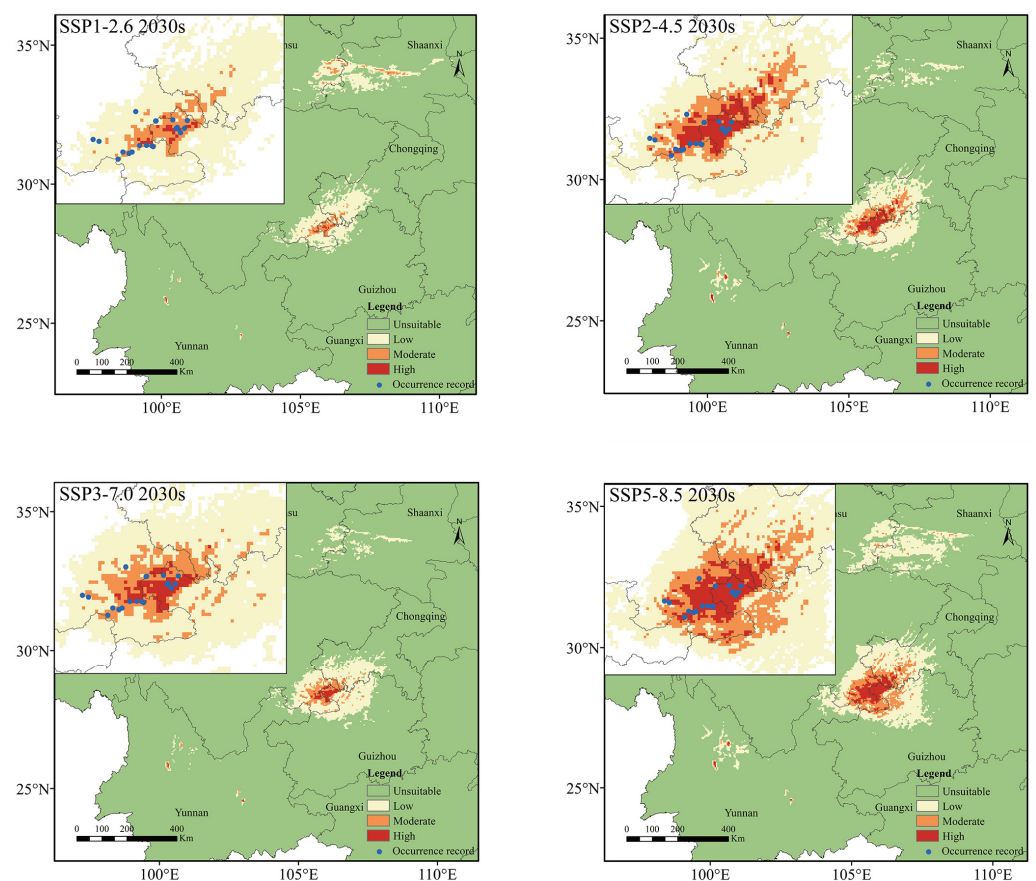


Figure 10. Projected potential distribution areas of *C. luteoflora* under four future climate scenarios.

Climate is the dominant factor affecting the geographical distribution of species at large scales in geographic regions [47]. Dai et al. concluded that mainly the mean temperature of the warmest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter were the dominant factors affecting the potential geographical distribution of *C. luteoflora*. This study found that the mean diurnal range, temperature annual range, and precipitation of the wettest month were the key environmental variables

influencing the potential geographic distribution of *C. luteoflora*, which is consistent with the ecological habitus of natural *C. luteoflora* that is often found in moist river valleys, streamsides or forests, and requires a warm, humid environment [13]. The difference in the results of the two studies is related to removing artificially introduced populations, adding new population distribution data and optimizing the model parameters in this study. In the prediction of the current potential distribution area of *C. luteoflora*, this study is basically consistent with the results of Dai et al. [18], but because the scope of Dai's study did not include Shaanxi and Gansu Provinces, the potential distribution areas of these two provinces were not included in their final prediction.

Recent studies have shown that, in the background of global warming, there may increase in the area where plant growth is limited by heat, triggering the migration of their biogeographic regions to higher latitudes or altitudes [48,49]. Climate warming may lead to a wetter climate at high latitudes and a more arid climate at mid-latitudes [45], making the suitable habitats of *C. luteoflora* shrink in parts of Sichuan and Guizhou provinces and then migrate to higher latitudes and altitudes in the north and southwest, which may be a strategy for *C. luteoflora* to respond to the changing environment. Furthermore, with the intensifying global warming, the suitable area for *C. luteoflora* began to gradually become fragmented as it shifted to higher latitudes and altitudes. Other plants species' potential distribution areas, such as of *Populus euphratica* Oliv. (Salicales: Salicaceae) and *Magnolia wufengensis* L.Y.Ma & L.R.Wang (Magnoliales: Magnoliaceae), also show a tendency to increase fragmentation as they move towards higher latitudes [50,51]. Hu et al. suggested that this might be mainly due to the constrained ecological adaptability that plants with small distribution areas usually have [52]. Habitat fragmentation is one of the primary threats to plant populations [53,54] as it reduces local population size and gene flow from other populations, thereby decreasing outcrossing rates, genetic variation, and adaptation to future climates [52,55]. Little is known about the extent to which habitat fragmentation affects the reproductive success and population viability of *C. luteoflora* and further experiments and explorations are needed.

Within the range of potential future suitable areas of *C. luteoflora*, in addition to the existing distribution areas located in southeastern Sichuan and northwestern Guizhou as the best suitable area, some areas of the Hengduan Mountains region also contain a certain scattered distribution. Geographic areas that are less affected by climate change and maintain relatively stable habitats can provide ideal natural environments for the survival and reproduction of organisms and maintain abundant genetic diversity or designate the areas of overlap between current and future suitable distribution as refugia [56]. The existing distribution area of *C. luteoflora* is quite rich in plant species, in which the East Asian endemic genus accounts for a relatively high proportion, with obvious characteristics of East Asian flora; phylogenetically in the primitive isolated position of the relics, the ancient plant taxa are numerous [57]. Due to its geological and historical genesis with the special ecological environment such as low terrain, high mountain barrier, high temperature and humidity, and good heat conditions which enable Theaceae, Fagaceae, and Lauraceae to develop and occupy obvious advantages [14], it also provides a suitable environment for the growth and development of *C. luteoflora*, where the existing area can be regarded as a potential biological refuge.

On the other hand, the Hengduan Mountains region, located on the southern and eastern margins of the Tibetan Plateau, has been recognized as the core area of the globally important Himalayan biodiversity hotspot [58]. The paleogeographic and paleoenvironmental location of the Hengduan Mountains, coupled with their complex seed plant flora characteristics and rich endemic species, has made them an important refuge for many rare, endemic, and ancient plants [59], as well as a hotspot for refuge research [60,61]. Although no specimens of *C. luteoflora* have yet been recorded in the Hengduan Mountains, the Hengduan Mountains region may also be the future climate refugia for *C. luteoflora* based on the implied dynamics of *C. luteoflora* geographic distribution under different climate scenarios.

Exploring the adaptation strategies of endangered species to respond to climate change can enable us to know the ecological risks they will face, which is important for formulating scientific conservation strategies [62]. Nature reserves have been established in Gulin, Changning, and Chishui. However, under future climate scenarios, the suitable habitats in southeastern Sichuan, northeastern Yunnan, northwestern Guizhou, and southwestern Chongqing will shrink in a circular pattern, resulting in a further reduction in the suitable habitats for *C. luteoflora*, which will further threaten the growth of the existing distribution points. In particular, the HSI of some populations (6th, 7th, 8th, 12th, and 21st distribution points) for *C. luteoflora* in Luzhou, Yibin, and Chishui continues to decrease and remain low, so there is an urgent need to focus on these potential extinction sites and to advance transplanting to the future higher suitability of the existing distribution areas in the vicinity. For the Hengduan Mountains region, where no specimens have been documented, the Hengduan Mountains region can also be used as an alternative site for transplanting *C. luteoflora* for ex situ conservation, following the example of *Bretschneidera sinensis* Hemsl. (Brassicales: Akaniaceae) which has been used to establish ex situ conservation in ecologically and climatically suitable areas [63].

In this study, the bioclimatic data of known distribution points were utilized as the environmental characteristics of the suitable habitat for *C. luteoflora*, thereby predicting the suitable habitat for the distribution of *C. luteoflora*. However, the prediction results in this study only represented the areas with similar environmental conditions to the existing areas without considering the natural and anthropogenic factors related to the distribution of *C. luteoflora*, so the prediction results had some deviation from the actual suitable distribution areas of *C. luteoflora*. In future studies, in addition to bioclimatic variables, factors such as the intensity of anthropogenic disturbances and associated socio-economic activities will be collected into the model to improve prediction accuracy. We also recommend that future studies should further predict the distribution pattern for *C. luteoflora* in response to historical climatic changes, trace the evolutionary history of its population, and clarify its needs for environmental factors, with the hope of providing more effective guidance for the developing conservation strategies for *C. luteoflora*.

5. Conclusions

In this study, by setting parameters (RM and FC) in the Maxent model, the parameter settings at FC = LPT and RM = 1.3 were determined to be the optimal model. The mean diurnal range, temperature annual range, and precipitation of the wettest month were key environmental variables affecting the distribution of *C. luteoflora*. Under current conditions, only 2.281% of the land was suitable for *C. luteoflora*. However, this study predicted that the growth of *C. luteoflora* in parts of Sichuan and Guizhou was disturbed and suitable habitats continued to shrink, further threatening the existing distribution points. The expansion of suitable habitat areas was mainly concentrated in Gansu and Shaanxi as well as the Hengduan Mountains region. In response to climate change, the potential range of *C. luteoflora* will shift partially to higher latitudes and the Hengduan Mountains and the centroid will move to the north and southwest. Based on the potential distribution areas and distribution dynamics of *C. luteoflora*, we hypothesize that the existing distribution areas and the Hengduan Mountains region may be future climate refugia for *C. luteoflora*, which is one of the key survival strategies for *C. luteoflora* to respond to climate change. The habitat suitability index of *C. luteoflora* at different time periods in the present and the future was used to more visually assess the suitability of *C. luteoflora* distribution points. As the climate warms the populations on the edge of extinctions, the current highly and moderately suitable habitats are vulnerable to climate change, and therefore, these populations should be prioritized for ex situ conservation. The Maxent model provides a basis for accurately assessing the adaptation and vulnerability of *C. luteoflora* to climate change as well as for developing scientific strategies to cope with the impacts of climate change and is also informative for the development of conservation and management measures for other endangered plants coping with climate change.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14112177/s1>, Figure S1. Omission rates and AICc values for all, non-significant, and selected “best” candidate models; Table S1. *C. luteoflora* screened geographic data for 17 distribution sites; Table S2. *C. luteoflora* geographic data for six distribution sites in Chishui.

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