



OPEN Predicting suitable habitat for the endangered tree *Ormosia microphylla* in China

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Climate change has significantly influenced the growth and distribution of plant species, particularly those with a narrow ecological niche. Understanding climate change impacts on the distribution and spatial pattern of endangered species can improve conservation strategies. The MaxEnt model is widely applied to predict species distribution and environmental tolerance based on occurrence data. This study investigated the suitable habitats of the endangered *Ormosia microphylla* in China and evaluated the importance of bioclimatic factors in shaping its distribution. Occurrence data and environmental variables were gleaned to construct the MaxEnt model, and the resulting suitable habitat maps were evaluated for accuracy. The results showed that the MaxEnt model had an excellent simulation quality (AUC = 0.962). The major environmental factors predicting the current distribution of *O. microphylla* were the mean diurnal range (bio2) and precipitation of the driest month (bio14). The current core potential distribution areas were concentrated in Guangxi, Fujian, Guizhou, Guangdong, and Hunan provinces in south China, demonstrating significant differences in their distribution areas. Our findings contribute to developing effective conservation and management measures for *O. microphylla*, addressing the critical need for reliable prediction of unfavorable impacts on the potential suitable habitats of the endangered species.

Keywords *Ormosia microphylla*, Climate change, MaxEnt model, Suitable area, Species distribution model (SDM), Conservation measure

Climate change has influenced the growth and survival of plant species, especially those with a narrow ecological niche^{1,2}. Extreme high temperatures and droughts, incurring abiotic and biotic stresses, can harm plant growth and forest health³. Moreover, changes in environmental conditions could alter physiological responses, metabolic processes, phenology, and seed dispersal. Plants may respond by adapting to the new conditions or shifting or shrinking their geographical range^{4,5}.

Consequently, climate change has brought far-reaching impacts on the distribution patterns of plant species in recent decades, constituting a primary cause of their decline and loss⁶. Temperature and precipitation changes brought by climate change modify plant physiological processes, affecting growth, development, reproduction, stability, and geographical distribution^{7,8}. Notable and fast climate change can induce serious degradation or loss of species habitats. Plants with weak adaptability and poor dispersal could be driven to local extinction⁹. Therefore, assessing climate change impacts on the distribution area and spatial pattern of threatened and endangered plants is crucial for monitoring and restoring native populations in their natural habitats. The results can enhance the formulation of sustainable conservation and management strategies to maintain habitat integrity¹⁰.

In recent years, species distribution modeling (SDM) (e.g., MaxEnt, Random Forests, Bioclim, and Climex) has emerged as an analytical tool for conservation planning and biodiversity management. It is especially useful in poorly surveyed regions beset by increasing habitat degradation and loss pressure^{11,12}. SDMs can integrate species occurrence data with environmental variables to simulate and predict habitats suitable for species growth and map the distribution of potential suitable habitats across space and time^{13,14}.

Among various SDM algorithms, the Maximum Entropy (MaxEnt) model combines machine learning and maximum entropy principles to predict the potential distribution areas of species^{15,16}. The method's many

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advantages have triggered extensive application to species distribution modeling. It can utilize both continuous and categorical data and incorporate interactions between variables. It performs better than similar models in forecasting species distribution with small sample size or presence-only data⁵. Additionally, the probability distribution obtained from Maxent has a concise mathematical expression, allowing direct generation of a habitat suitability map¹⁷. Each environmental variable's relative importance (%) can be evaluated using the software's built-in jackknife test¹⁸. These MaxEnt capabilities provide an effective way to predict the potential distribution of endangered species, which often have a limited number of observed occurrences and grow in remote areas with terrain and access constraints, making field data collection difficult¹⁹.

Ormosia microphylla (Merr. & H. Y. Chen) is a dioecious tree species of the Fabaceae family. It is a first-class national protected plant in China. This evergreen tree can reach 15–20 m in height. The legume fruits ripen from October to November. Each fruit holds 3–4 extremely hard seeds that are brightly colored in shades of red. The seeds (150–180 g/1000 grain) rely on wind dispersal. Importantly, the species has high economic value. The attractive seeds are used in jewelry and handicrafts. The priced wood, strong and heavy with handsome grain, is used for furniture and flooring, constituting the main reason for its extensive logging²⁰.

The natural distribution range of *O. microphylla* is very narrow. It is restricted to forests at 600–800 m altitude on slopes and foot slopes in central and south China, covering Guizhou, Hunan, Guangxi, Guangdong, and Fujian provinces²¹. Moreover, the species is beset by low genetic diversity, poor natural regeneration ability, and low seed germination rate, which have jointly depressed its population growth, density, and distribution. Unfortunately, its high economic value, mainly as a valuable timber source has incurred excessive felling by humans. Consequently, the species has suffered from massive tree losses, a severely fragmented range, and increasing scarcity in the wild²².

Previous *O. microphylla* studies have focused on its population structure²², with little attention on geographical distribution and factors influencing its habitat. However, its habitat has been seriously damaged, and the natural distribution area has been drastically reduced due to the acute impacts of climate change and human disturbance. Therefore, it is important to study the potential impacts of climate change on the species to yield information about its distribution range, habitat preference, and population dynamics.

This study aimed to investigate the suitable habitat distribution of *O. microphylla* in China with two research objectives: (1) to predict the current potential spatial distribution; and (2) to identify the key environmental factors highly correlated with *O. microphylla* distribution range. The findings will be useful in developing conservation and management measures for the species.

Materials and Methods

Establishing species occurrence records

Occurrence data of *O. microphylla* in China were obtained from the Chinese Virtual Herbarium (<http://www.cvh.ac.cn>), Plant Photo Bank of China (<http://www.Plantphotophoto.cn>), National Specimen Information Infrastructure (<http://www.nsii.org.cn/>), field surveys, and the published literature. Each occurrence record was scrutinized for data quality and suitability with reference to the model's requirements. Records with unclear latitude and longitude information and duplicated distribution points were discarded. A total of 45 verified distribution points of *O. microphylla* were kept for final analysis to generate the potential distribution based on MaxEnt modeling. The occurrence-point data were stored in a CSV file, sorted by species name, longitude and latitude, and plotted on a map (Fig. 1).

Selecting environmental variables

Data on 19 bioclimatic parameters, including monthly temperature and precipitation, were selected and downloaded from the WorldClim website (<http://www.worldclim.org>) (Table 1). The comprehensive climatic data from 1950 to 2000 were based on monthly meteorological data harvested from different weather stations worldwide. The raw climatic data were interpolated according to a grid with a 2.5-arcminute resolution to generate the global spatial dataset. The rather general annual temperature and precipitation variables were deleted from the dataset^{23,24}. Strong correlation among the environmental variables can lower model accuracy. Therefore, Pearson's correlation coefficients (r) were calculated between variable pairs. Variables reaching $|>0.8|$ were removed to avoid multicollinearity impacts²⁵. Ultimately, we shortlisted eight variables to construct the MaxEnt model for *O. microphylla* in this study.

To avoid model overfitting, the “ENMeval” software package in R 4.0.2 was employed to optimize MaxEnt model²⁶. For optimization, regular Multiplier (RM) and Feature Class (FC) were included in MaxEnt. RM could smooth the model and minimize model over-fitting. FC, corresponding to the response type of suitability values to each variable, could determine the potential shape of response curves, including Linear (L), Product (P), Quadratic (Q), Threshold (T), and Hinge (H)²⁷. In the process of parameter optimization, the RM value ranged from 0.5 to 4.0 with an increment of 0.5. Six combinations of FCs (L, LQ, LQP, LQT, QPT, PHT) were selected. Combined with the 8 values of RM, this resulted in a total of 48 parameter combinations. The 48 parameter combinations were input into ENMeval for comprehensive testing. We used the delta from the Akaike information criterion (AIC), AICc, the difference between training and testing AUC (AUC.DIFF) and the 10% training omission rate (OR10) to evaluate the model's fitting degree and complexity on species distribution²⁸.

Modeling species distribution

The eight selected environmental variables and species occurrence records of *O. microphylla* were loaded into MaxEnt 3.3. Then, 75% of the distribution points were randomly selected as testing data to establish the prediction model, and the remaining 25% were used to verify the model's accuracy. To avoid the instability caused by randomly selected data, the initial operation of the model was repeated ten times. A Jackknife test was applied to

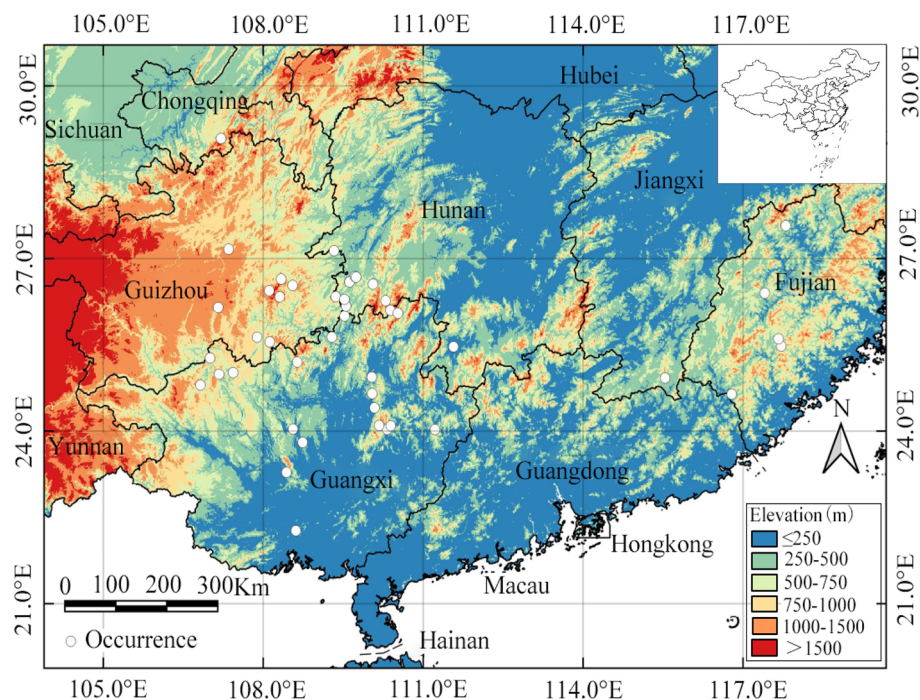


Figure 1. The locations of 45 verified current occurrence points of *O. microphylla* (white circles) in central and south China with reference to elevation. The map was prepared by Lijuan Wei, Guohai Wang and Chunping Xie in QGIS 3.34.0 (<https://www.qgis.org/en/site/>).

Code	Environmental variable	Unit
bio1	Annual mean temperature	°C
bio2	Mean diurnal range (mean of monthly (max temp-min temp))	°C
bio3	Isothermality (bio2/bio7) (*100)	-
bio4	Temperature seasonality (standard deviation*100)	°C
bio5	Max temperature of the warmest month	°C
bio6	Min temperature of the coldest month	°C
bio7	Temperature annual range (bio5-bio6)	°C
bio8	Mean temperature of the wettest quarter	°C
bio9	Mean temperature of the driest quarter	°C
bio10	Mean temperature of the warmest quarter	°C
bio11	Mean temperature of the coldest quarter	°C
bio12	Annual precipitation	mm
bio13	Precipitation of the wettest month	mm
bio14	Precipitation of the driest month	mm
bio15	Precipitation seasonality (coefficient of variation)	-
bio16	Precipitation of the wettest quarter	mm
bio17	Precipitation of the driest quarter	mm
bio18	Precipitation of the warmest quarter	mm
bio19	Precipitation of the coldest quarter	mm

Table 1. List of 19 environmental variables considered at the initial stage of model development. Eight variables with the code shown in bold font were chosen for the MaxEnt modeling study.

measure the relative importance of each variable on the distribution of this species by percent contribution to the overall model fit and permutation importance. Permutation importance represents how heavily the final model depended on a certain variable²⁹ and was calculated by random values of each variable between presence and background points and then measures resulting drop in AUC with a larger drop indicating higher importance of that variable to the model^{30,31}. Then, the receiver operating characteristic (ROC) curve and the area enclosed by the abscissa as the area under the curve (AUC) were used to evaluate model accuracy²⁴. The AUC value ranges

from 0.5 for an uninformative model to 1 for perfect discrimination³². An AUC value close to 1 indicates more habitat suitability deviation from a random value and a stronger correlation between environmental variables and habitat classification, signifying a better model prediction^{33,34}. The suitable habitat maps were calculated using the logistic output of MaxEnt, which ranges from 0 to 1.

The outputs of the MaxEnt model in logistic format were imported into QGIS software for data extraction. China's map served as the base to extract the potential suitable distribution of *O. microphylla*. The average logical value combined with the actual distribution were used to classify distribution-level values and corresponding distribution ranges. The specific suitability is divided into five categories: fail (0–0.15), poor (0.15–0.3), fair (0.3–0.45), good (0.45–0.6), and excellent (>0.6)^{35,36}. Different suitable levels indicate the differential potential distribution probability of the species in specific areas. The higher the probability, the more suitable is an area for species occurrence.

Results

Evaluating model performance

The current distribution areas of *O. microphylla* were predicted using the MaxEnt model (Fig. 2). The AUC value for the MaxEnt models was 0.962, which was significantly higher than the AUC value of a random prediction (0.5). This result indicated that the prediction results were “excellent”, and the MaxEnt model was reliable for predicting the potential geographical distribution areas of *O. microphylla* in China.

Key environmental factors and validation of modeling results

The key environmental factors shaping the potential distribution of *O. microphylla* were determined according to their contributions to the MaxEnt modeling process by the jackknife test (Table 2). It found that bio14 (precipitation of the driest month), bio4 (temperature seasonality), and bio16 (precipitation of the wettest quarter) had the highest contribution of 53.3%, 22.6% and 12.2%, respectively (aggregate contribution of 88.1% to the

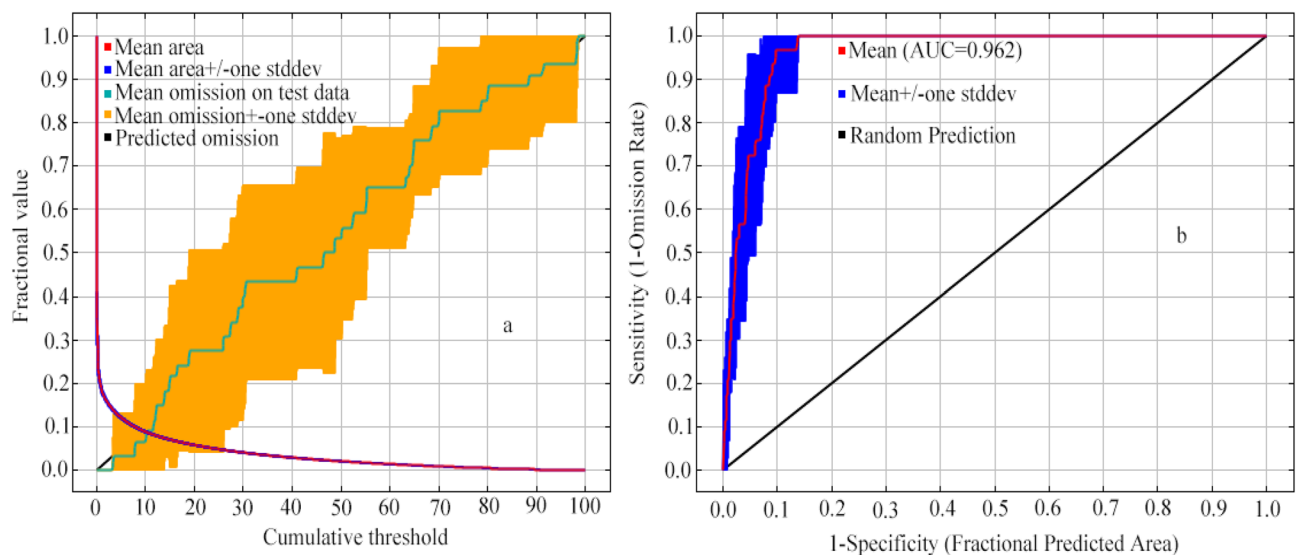


Figure 2. The validation of the MaxEnt model predicting *O. microphylla* distribution: (a) Omission rate; and (b) ROC curve.

Code	Bioclimatic variable	Percent contribution (%)	Permutation importance (%)
bio14	Precipitation of the driest month	53.3	38.0
bio4	Temperature seasonality	22.6	6.8
bio16	Precipitation of the wettest quarter	12.2	1.0
bio2	Mean diurnal range	3.7	45.8
bio10	Mean temperature of the warmest quarter	2.9	2.1
bio3	Isothermality (Bio2/Bio7) (*100)	2.2	2.5
bio11	Mean temperature of the coldest quarter	2.0	1.2
bio15	Precipitation seasonality	1.1	2.6

Table 2. Percent contribution and permutation importance levels of the eight environmental variables included in the MaxEnt models, ranked by percentage contribution.

model; Table 2). The mean diurnal range (bio2, 45.8%) and precipitation of the driest month (bio14, 38%) had the highest permutation importance. The correlation coefficients (r) between the eight environmental factors were below 0.8. The two bioclimatic factors (bio14, bio2) were identified as the main drivers of the modern geographical distribution of *O. microphylla*.

The results of jackknife tests indicated that when only individual variables were used, the regularized training gain, test gain, and AUC values of the mean diurnal range (bio2) and precipitation of the driest month (bio14) declined the most. These two variables, demonstrating the strongest influence on species distribution, were the main factors influencing the geographical distribution of *O. microphylla* (Fig. 3).

The species response curve depicts the relationship between environmental variables and the probability of species incidence. They show the target species' biological tolerances and habitat preferences. The distribution probability of *O. microphylla* increased with the value of each environmental variable within a certain range. It decreased with the increase of the variable after reaching a certain peak value (Fig. 4). Based on the species response curves, *O. microphylla* prefers the mean diurnal range (bio2) range from 7 to 8°C, and precipitation of the driest month (bio14) ranges from 30 to 40 mm (Fig. 4).

Predicting suitable habitats of *O. microphylla* in China

The five categories of *O. microphylla* suitability habitats for the current climate were mapped (Table 3 and Fig. 5). The suitable areas for the fail, poor, fair, good, and excellent suitability categories occupied $183.67 \times 10^4 \text{ km}^2$, $41.76 \times 10^4 \text{ km}^2$, $23.19 \times 10^4 \text{ km}^2$, $17.42 \times 10^4 \text{ km}^2$, and $16.55 \times 10^4 \text{ km}^2$, respectively, comprising 19.13%, 4.35%, 2.42%, 1.81%, and 1.72% of China's total land area (about $960 \times 10^4 \text{ km}^2$) (Table 3). The excellent suitable habitat areas were mainly distributed in the south China provinces of Guangxi, Guizhou, Hunan, Guangdong, and Fujian, covering approximately $14.59 \times 10^4 \text{ km}^2$ (Table 3). However, the provinces contiguous or proximal to the main distribution areas, namely Hubei, Zhejiang, and Taiwan, have no distribution records in the good and excellent categories. This pronounced discrepancy indicates that the potential range of *O. microphylla* is considerably larger than the actual distribution range, and the species has the potential to expand the current range to fill the potential areas.

Discussion

This is the first study employing the MaxEnt model in conjunction with QGIS to analyze the spatial distribution pattern of *O. microphylla* and climate change impacts on its potential geographical range, and predict its potential distribution area in China quantitatively and intuitively. We built the model with 45 valid occurrence records and eight key environmental factors (Fig. 1). The AUC value generated by MaxEnt reached 0.962 (Fig. 2), indicating the prediction had a high degree of fit between the climatic variables and the actual suitable habitat of *O. microphylla*. The model jackknife test provided a measure of the contribution of the various environmental variables in influencing the suitability for *O. microphylla*. The prediction results provide a theoretical basis for developing protection and management measures for the endangered species.

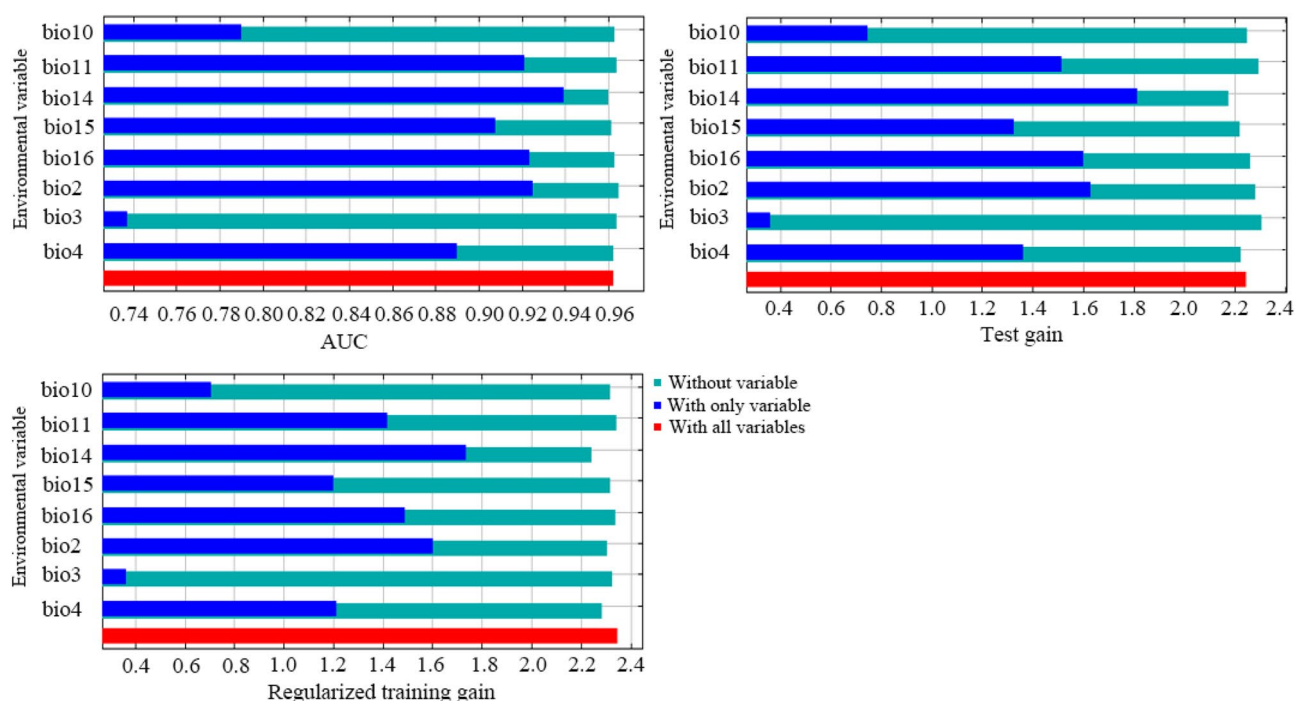


Figure 3. The jackknife test for evaluating the relative importance of environmental variables for *O. microphylla*.

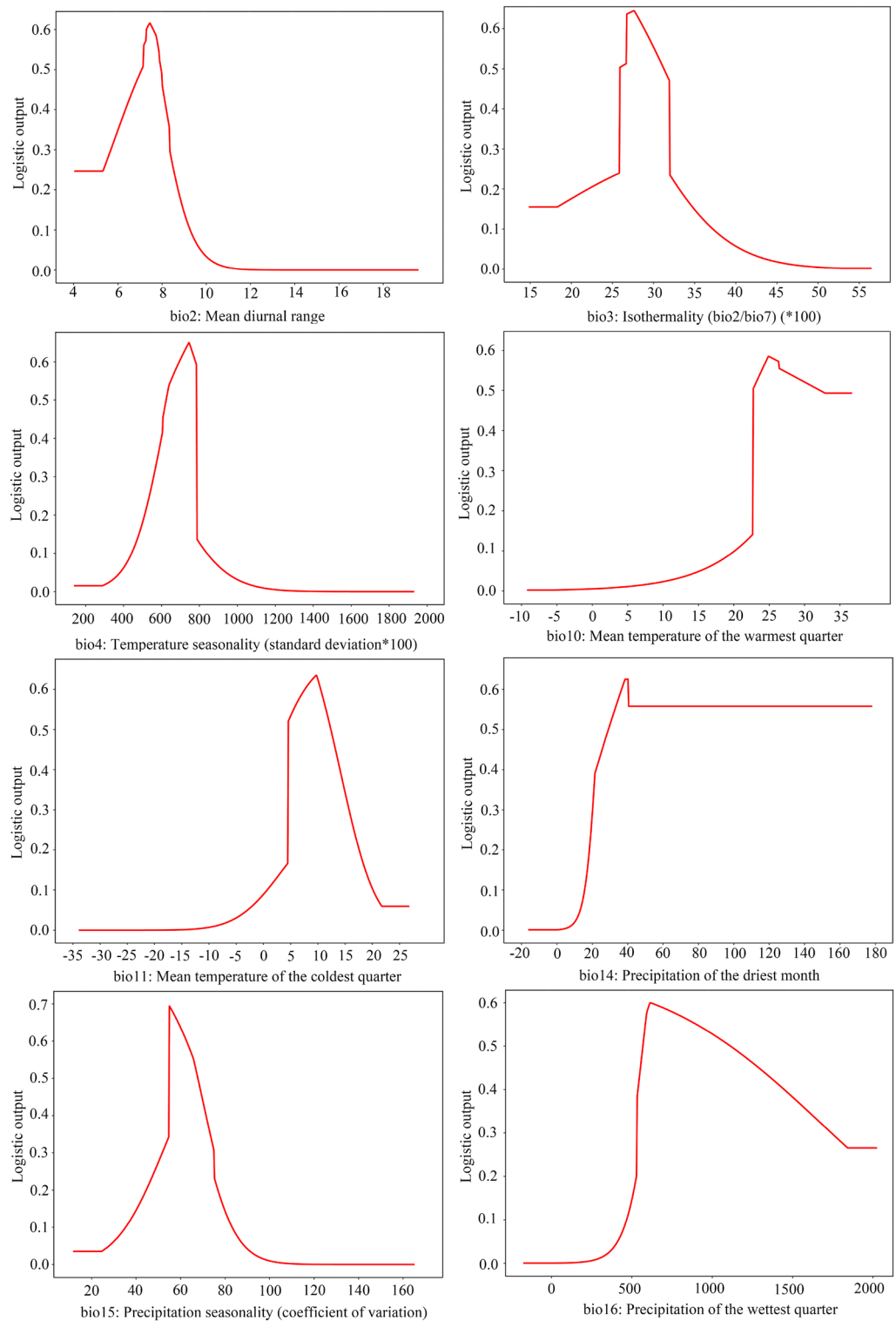


Figure 4. Response curves of the environmental variables to distribution probability.

This study analyzed the relationship between the occurrence probability of *O. microphylla* and key environmental variables. The results showed that precipitation of the driest month (bio14) was the primary bioclimatic variable affecting the presence of *O. microphylla*, with optimum conditions at 30 to 40 mm. As a plant growth prerequisite, precipitation is the primary limiting factor for almost all species^{37,38}. Variations in precipitation and consequent changes in temperature and humidity disrupt the balance of soil moisture and most physiological plant functions^{36,39}. The driest month in China occurs in March, April, or May, accompanied by higher temperatures. Moreover, this Spring season is critical for the germination of *O. microphylla* seeds. Sufficient precipitation

Province	Probability of prediction				
	Fail (0–0.15)	Poor (0.15–0.3)	Fair (0.3–0.45)	Good (0.45–0.6)	Excellent (>0.6)
Guangxi	4.06	6.09	4.68	4.47	4.46
Fujian	0.18	1.41	2.82	3.88	3.86
Guizhou	3.12	5.55	3.90	2.30	2.75
Guangdong	3.67	6.91	3.72	1.68	1.98
Hunan	12.58	4.35	1.58	1.14	1.54
Jiangxi	9.16	2.73	2.01	1.84	0.95
Zhejiang	4.77	2.42	1.10	0.99	0.89
Hubei	15.06	1.35	1.48	0.60	0.10
Taiwan	1.62	0.90	0.72	0.36	0.01
Chongqing	3.48	3.39	1.22	0.16	0.01
Sichuan	45.24	2.96	0.40	0.00	0.00
Yunnan	38.7	0.57	0.14	0.00	0.00
Anhui	12.11	1.77	0.13	0.00	0.00
Jiangsu	9.45	1.27	0.00	0.00	0.00
Shanxi	20.47	0.09	0.00	0.00	0.00
Total	183.67	41.76	23.19	17.42	16.55

Table 3. Predicted suitable areas for *O. microphylla* under the current climate scenario in various provinces (10^4 km²). The ratio denotes the predicted suitable area divided by the total land area of the respective province or autonomous.

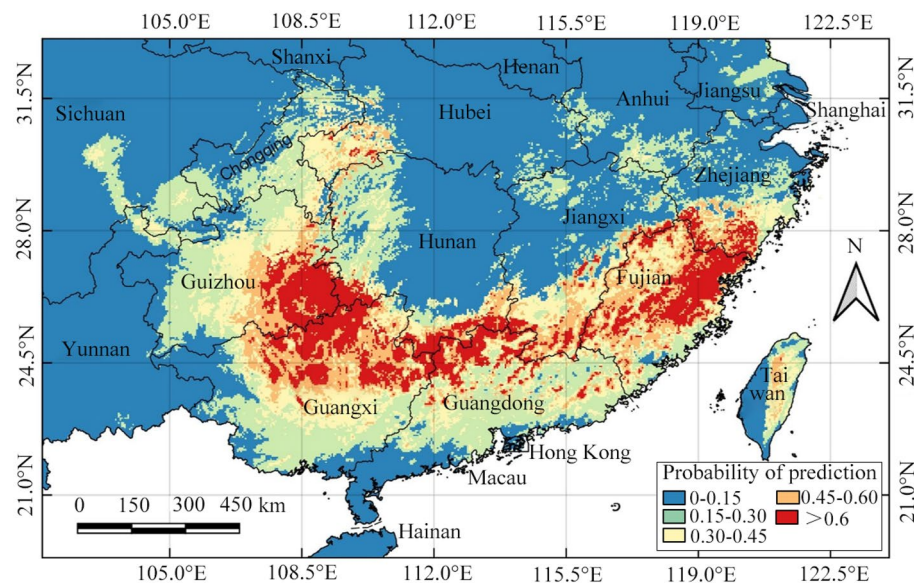


Figure 5. The predicted *O. microphylla* distribution range classified into five suitability categories obtained by MaxEnt modeling. The map was prepared by Lijuan Wei, Guohai Wang and Chunping Xie in QGIS 3.34.0 (<https://www.qgis.org/en/site/>).

of the driest month can raise atmospheric humidity and soil moisture to foster seed germination and seedling growth. Nevertheless, little is known about how precipitation affects the survival of *O. microphylla*, and future extensive research could tackle this question.

The MaxEnt model found divergent relative importance for the eight environmental variables. The mean diurnal range (bio2) was the principal temperature variable limiting the potential suitable distribution of *O. microphylla* (Table 2 and Fig. 3), with optimum conditions at 7–8 °C (Fig. 4). The mean diurnal range denotes the temperature variations in a day, which may impact plant growth, especially daytime photosynthesis and respiration that contribute to nutrient buildup⁴⁰. Some pertinent processes associated with photosynthesis are highly sensitive to temperature. Low temperatures can reduce the hydrolysis and transport of starch accumulated within the chloroplast to depress the photosynthetic rate. It can also suppress the germination rate and biomass accumulation and modify the survival strategies. On the contrary, the photosynthetic rate increases in response

to temperature rise until reaching a thermal optimum, after which the rate declines due to enzyme deactivation at high temperature^{41,42}. Other studies have shown faster temperature rises at nighttime than daytime, which is not conducive to nutrient accumulation^{43,44}. However, the specific mechanism concerning the influence of mean diurnal range on *O. microphylla* is unclear. Therefore, research on this topic could be strengthened in the future.

The other variables, such as bio4 (temperature seasonality) and bio16 (precipitation of the wettest quarter), have an important influence on the habitat suitability distribution of *O. microphylla* (Table 2). Temperature seasonality represents the temperature variations in a year. A larger standard deviation brings a greater coefficient of variation⁴⁵. Therefore, this species is not suitable for an environment with a wide annual temperature amplitude. The wettest period in China occurs in June, July, and August, which also have the highest yearly temperatures⁴⁶. Moreover, this Summer season is also a critical period for the maturation of *O. microphylla* fruits and seeds. Sufficient precipitation in the wettest quarter can raise atmospheric humidity and soil moisture to foster fruit growth and maturation. The moist conditions also increase fats and soluble sugars in seeds, boosting the energy supply for germination and initial seedling growth. The ability of seedlings in different habitats to resist harsh environmental conditions will be correspondingly enhanced⁴⁷.

Under current climate conditions, the excellent suitable habitats for *O. microphylla* mainly cover Guangxi, Guizhou, Hunan, Guangdong, and Fujian provinces in south China (Table 3 and Fig. 5). The model's prediction matches the existing data, highlighting the accuracy of the prediction. However, the predicted suitable habitat is much larger than the current known species distribution. No occurrence record is found in Sichuan, Yunnan, Hubei, Anhui, Zhejiang, Jiangsu, and Taiwan provinces, even though they are the species' potentially important habitats. This notable discrepancy may be related to limited research on this species, resulting in inadequate data to describe species environmental requirements accurately. On the other hand, MaxEnt has the inherent trait of evaluating only niche-based species presence data⁴⁸. The model predicts the species' fundamental niche rather than the actual niche, resulting in the predicted potential distribution area being larger than the actual range. However, the species may fail to disperse to some suitable areas due to biogeographical barriers, such as human interference, topographical obstacles, and inter-specific competition⁴⁹.

Based on the predicted results, the suitable habitat of *O. microphylla* is relatively widespread. However, in reality, the prospect of population development is not optimistic. To prevent the extinction of this endangered plant, in situ conservation of the known *O. microphylla* community is necessary to minimize the adverse effects of human activities on species survival. More distribution point information can be obtained by conducting *O. microphylla* studies to deepen the knowledge of biological characteristics, genetic structure, and artificial cultivation methods, as well as investigating and monitoring the apparent "omission" areas. Collecting seeds for artificial breeding and selecting potential suitable areas with less human activity for wild release can expand the spread and size of wild populations.

The ability of the MaxEnt model to use scarce distribution records to infer the environmental tolerance and ecological niches of *O. microphylla* is supported by the generation of highly accurate predictions. However, it was difficult for the species to establish and survive in all suitable areas. The distribution areas of its communities have been progressively reduced despite the expansion of suitable habitats⁵⁰. Besides external environmental and climatic conditions, other factors may have important implications for species distribution at different spatial scales⁵¹. They include physiological constraints, topography, soil, human disturbance, spatial constraint, dispersal mode, competition, and response to external factors and drivers. For instance, the seeds of *O. microphylla* are hard and compact, with a less permeable cortex and a long dormancy period. Thus, its germination rate is extremely low, making it difficult to survive in suitable areas⁵¹. In addition, land use and land cover changes caused by human activities have significantly impacted species distribution⁵². However, these factors take time to take effect, which may cause species distribution to lag behind climate change⁵³.

Under the climatic conditions of increasing CO₂ concentration and temperature in the future, the annual mean precipitation may increase across China⁵⁴. Our research showed that the main factors influencing the distribution of *O. microphylla* were the mean diurnal range and precipitation of the driest month. With the increase of temperature and precipitation in the future climate change, sufficient soil moisture and suitable soil temperature can better meet the needs of seed germination and vegetation growth⁵⁵. Therefore, the suitable area of *O. microphylla* may vary with the magnitude of future climate change.

In short, predicted results based on the MaxEnt model could help identify additional localities where the *O. microphylla* may already exist but have not yet been detected. Alternatively, the predicted suitable areas offer new habitats to expand the species range or are used as priority areas for introducing and cultivating this rare tree. Therefore, deeper cognate research should be conducted to expand the knowledge and practice base. The locations of key protected areas for *O. microphylla* could be identified to strengthen their supervision and management and minimize human activities. Uninformed and subjective designation of protection areas can be avoided. The numerical range of the main environmental variables can provide an objective reference to select artificial breeding and rescue sites. Thus, the protected plants can be nurtured in appropriate environmental conditions to rationalize resource development and utilization. Moreover, this study indicates that other aspects can be improved. In addition to the selected bioclimatic variables, other factors such as soil, water, land use change, different climate scenarios, and dispersal ability may affect the prediction results. Therefore, future studies can comprehensively consider a broader range of environmental factors to develop a response strategy for *O. microphylla* to tackle climate change impacts.

Conclusion

The suitable areas of *O. microphylla* in China have been accurately predicted by MaxEnt modeling using mainly bioclimatic variables. The excellent and good suitable habitats were found primarily in China's southern provinces, including Guizhou, Hunan, Guangxi, Guangdong, and Fujian provinces. The crucial environmental

variables regulating its distribution are the precipitation of the driest month (bio14) and mean diurnal range (bio2), with the optimal conditions at 30–40 mm and 7–8 °C, respectively. The results could pinpoint the specific conditions and locations for the optimal growth of the species and provide the scientific basis to improve the management and conservation measures for this endangered species.

Data availability

The data presented in this study are available on request from the first author.

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Competing interests

The authors declare no competing interests.

Additional information

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