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Predicting Suitable Habitats for China's Endangered Plant *Handeliodendron bodinieri* (H. Lév.) Rehder

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Abstract: Demarcating a plant species' actual and potential biogeographical distribution is crucial for understanding the key environmental variables shaping its habitat conditions. We used MaxEnt and species distribution modeling to predict the likely range of China's endangered species, *Handeliodendron bodinieri* (H. Lév.) Rehder, based on forty-four validated distribution records and eight selected environmental variables. Combined with percentage contribution and permutation importance, the jackknife statistical method was applied to test and evaluate pertinent factors restricting the potential distribution of *H. bodinieri*. The response curves of critical bioclimatic factors were employed to determine the potential species range. The generated MaxEnt model was confirmed to have excellent simulation accuracy. The current core potential distribution areas are concentrated in the Guangxi and Guizhou provinces of Southwest China, with a significant inter-regional difference. The precipitation of the warmest quarter (Bio18) and minimum temperature of the coldest month (Bio6) had the greatest impact on the distribution area of *H. bodinieri*. The findings could provide useful information and a reasonable reference for managers to enhance the protection of this declining species.

Keywords: *Handeliodendron bodinieri*; MaxEnt; species distribution model (SDM); environmental factor; potential range

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1. Introduction

Climate change has become the biggest threat to protecting and maintaining global biodiversity [1,2]. Global warming and drought constitute the main climate change stressors on biota. The fundamental abiotic alterations disturb or damage species' habitats by changing the cardinal environmental attributes of temperature and precipitation [3,4]. Nature responds by modifying the structure, function and composition of biological communities and species distribution patterns at different scales [5,6]. In extreme cases, the diversity and stability of local and regional ecosystems could be disrupted and endangered [7].

Climate change has wrought far-reaching impacts on a broad range of plant functions and physiological processes. They include regeneration, growth pattern, morphology, anatomy, and reproductive behavior, which are key determinants of plant species distribution on a large scale [8,9]. These harmful and aberrant influences have accelerated shifting, contraction and fragmentation in the global geographical distribution patterns of many plant species. The changes have induced migration, reproductive failure and a raised mortality rate, thus increasing the number of globally endangered plant species [10]. Moreover, the survival of existing endangered plant species could be jeopardized due to straining beyond the tipping point [11].

The cumulative and serious impacts of climate change have disrupted the stability and operation of ecosystems [12,13]. For example, drastic short-term changes could kill individuals with weak adaptability and poor dissemination ability. The affected species would experience range shrinkage and local extinction [14]. Therefore, understanding the intricate relationships between potential suitable distribution patterns of endangered plants and environmental factors is critical for conservation. The knowledge can foster the monitoring and restoration of declining populations, improve resource management, and assess and abate anthropogenic impacts [15,16].

Species distribution models (e.g., MaxEnt, Garp, Bioclim, and Climex) are important tools to assess climate change's impacts on altering the distribution of suitable areas for plant species [17,18]. These models can establish a connection between a species' geographical distribution and environmental variables through statistical response functions. The analysis can predict potential suitable areas and future species distribution at different times in climate change scenarios [19,20]. Among these modeling approaches, the Maximum Entropy (MaxEnt) model is one of the most popular for modeling plant species distributions and their environmental niches. Its common adoption can be attributed to parsimonious data requirements, using only categorical and presence data as input variables for the species in question [21,22]. In addition, even with small sample sizes and data gaps, its forecast precision can remain stable and reliable [23,24]. The method can directly generate a spatially open habitat suitability map and evaluate the significance level of individual environmental variables using a built-in jackknife test [25,26]. The MaxEnt has been widely applied to different research fields, including conservation, ecology and evolution. More importantly, it has been employed to identify ecological niches and compare niche similarities between species pairs in geographic and environmental space [27,28].

Handeliodendron bodinieri (H. Lév.) Rehder (Sapindaceae) is a rare native monotypic plant species endemic to China. The range of the endangered small tree is confined to the karst region of the northwest Guangxi and south Guizhou provinces in Southwest China at a 500–900 m altitude [29]. This species is a semi-deciduous broad-leaf tree reaching up to 20 m in height. Its flowers are unisexual, with an aborted stamen or pistil in dioecious trees [30]. Although female plants bear fruits every year, the fruit abortion rate is high, resulting in poor natural regeneration. The oil-rich seeds are heavily consumed as food by granivorous wild animals, including invertebrates and rodents, which constitutes an important reproductive deprivation [31]. Another cause of population decline is excessive human seed collection to meet industrial and food uses, including for biodiesel extraction, as a source of protein, and as edible oil [30]. It is also harvested for its fine timber to make high-quality furniture. The natural and human pressures have jointly contributed to its continual decline.

In addition, the karst terrain is characterized by a finely divided mosaic of steep rocky hills and outcrops, with skeletal soil interrupted by depressions with thick and fertile soils. The physical environment comprises a varied habitat patchwork marked by considerable spatial heterogeneity in soil, water, and nutrients. The considerable habitat fragmentation is unfavorable to seed germination, rendering the species vulnerable to extinction. With a shrinking fragmented range, a small declining wild population, and intensification of negative forces [32], the endangered tree has been designated a second-level protected species under the List of National Key Protected Wild Plants (2021) in China (https://www.gov.cn/zhengce/zhengceku/2021-09/09/content_5636409.htm, 1 July 2023). The species has received extensive scientific investigations regarding population structure, spatial distribution, phytochemistry, reproductive ecology, genetic diversity, propagation, and population conservation [30,33]. Habitat fragmentation and drought stress have been increasingly recognized as important factors in protecting endangered species in China's karst landscape. Excessive human seed collection has decimated living plants and degraded the quantity and quality of soil seed banks. Therefore, it is necessary and important to predict how global climate change will impact the potentially suitable distribution of *H. bodinieri* in China.

This study aimed to explore the suitable habitat distribution of *H. bodinieri* at the regional scale and focused on the following aims: (1) to define and demarcate the potential spatial distribution pattern; (2) to determine the correlation between the potential suitable distribution pattern and environmental factors.

2. Materials and Methods

2.1. Establishing Species Occurrence Records

The research data are the occurrence records of *H. bodinieri* from 1930 to 2019. They were collected from the Chinese Virtual Herbarium (http://www.cvh.ac.cn (accessed on 6 July 2023)), the Plant Photo Bank of China (http://www.Plantphotophoto.cn (accessed on 6 July 2023)), the National Specimen Information Infrastructure (http://www.n-sii.org.cn/ (accessed on 6 July 2023)), and the published literature. Each record was scrutinized for data quality and suitability. Duplicated records and those with unclear latitude and longitude information were rejected. Finally, 44 valid occurrence records of *H. bodinieri* were included in this study. The longitude and latitude data of geographic distribution points were obtained from ArcGIS (10.2). The distribution points were stored in a CSV file sorted by species name and longitude, and latitude of the distribution points (Figure 1).

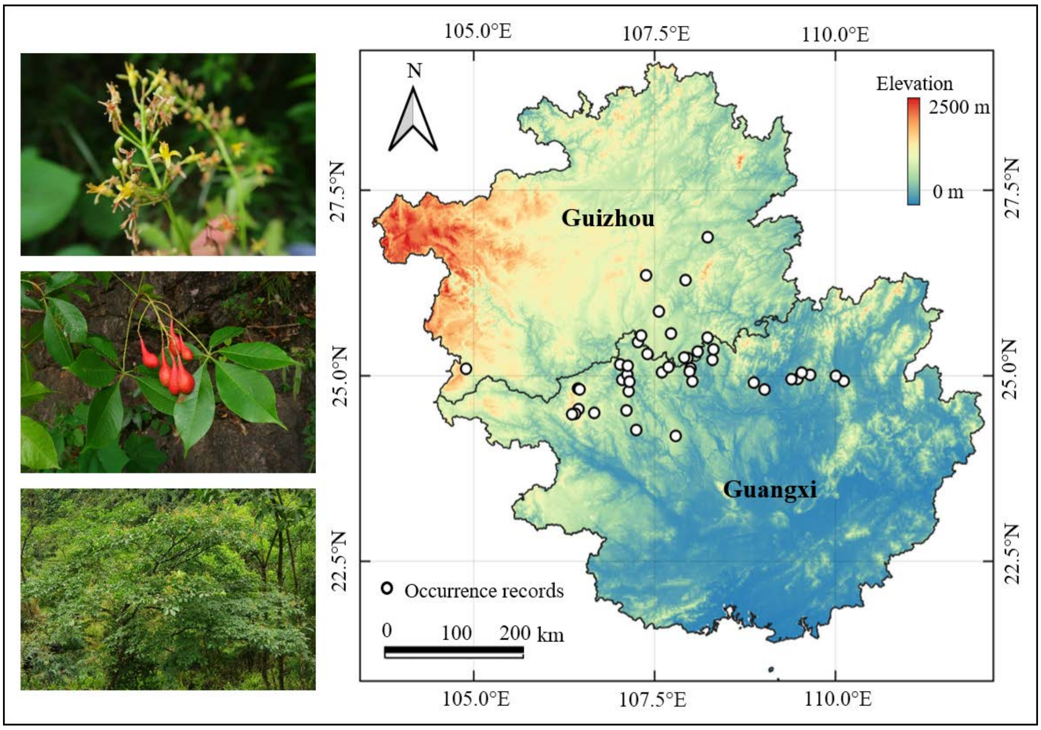

Figure 1. The images of *H. bodinieri* and its actual distribution area (white circles) in two provinces of Southwest China. The pictures on the left side show the flowers, fruits, and complete plants of the *H. bodinieri* from top to bottom.

2.2. Selecting Environmental Variables

Nineteen bioclimatic variables, including bioclimatic parameters, monthly temperature and precipitation data, were extracted from the WorldClim database, version 2.0 (http://www.worldclim.org (accessed on 6 July 2023)) using the 'Extract value by points' function in DIVA-GIS 7.5 [34] (Table 1). The annual temperature and precipitation variables, considered too general, were deleted from the dataset [35,36]. Pearson correlation coefficients (r) between environmental variables were calculated. The strongly associated environmental factors $|r > 0.8|$ were removed to reduce model overfitting due to multicollinearity and improve simulation accuracy [37,38]. Ultimately, eight of the nineteen variables were retained as evaluator variables.

Table 1. List of environmental variables considered in the course of model development. The eight variables with the code in bold font were chosen for the MaxEnt modeling study.

Code	Environmental Variable	Unit
Bio1	Annual mean temperature	°C
Bio2	Mean diurnal range (mean of monthly (maximum temp-minimum temp))	°C
Bio3	Isothermality (Bio2/Bio7) (×100)	-
Bio4	Temperature seasonality (standard deviation×100)	°C
Bio5	Maximum temperature of the warmest month	°C
Bio6	Minimum 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

2.3. MaxEnt Modeling of Species Distribution

The eight selected environmental variables and species occurrence records of *H. bodinieri* were loaded into MaxEnt 3.3. The package "ENMeval" of R 4.02 was used to create and evaluate the models [39,40]. For diverse environmental variables used in prediction, the jackknife test yielded training, test, and area under the curve (AUC) gains for three scenarios (without variables, with only one variable and with all variables). Then, the AUC of the receiver operating characteristic curve (ROC) was calculated to measure the accuracy of the generated models [36]. The AUC value has a range of 0–1. A higher AUC value indicates a considerable deviation in the geographic distribution of the simulation object from a random distribution. It also means a stronger correlation between the simulation result and the environmental variables, i.e., the model has a better prediction accuracy [41]. The AUC statistic is classified into five performance categories: excellent (0.9–1.0), good (0.8–0.9), fair (0.7–0.8), poor (0.6–0.7), and fail (0.5–0.6) [42]. Based on the optimal threshold of environmental factors (occurrence-probability) generated by MaxEnt, the final output with a 0–1 range was divided into five potential distribution areas using the reclassify tool of ArcGIS software: fail (0–0.15), poor (0.15–0.3), fair (0.3–0.45), good (0.45–0.6), and excellent (>0.6) [38,41].

3. Results

3.1. Evaluating Model Performance

The lines of omission from the training data were close to forecasted omission rates in the model, signifying the correct fitting of the training data, and the test and training data were unique (Figure 2a). The AUC value for the reconstructed MaxEnt was 0.99 (Figure 2b), indicating excellent prediction accuracy of the model, including the selected variables. This model is assessed to be reliable for defining suitable areas for introducing *H. bodinieri* in China.

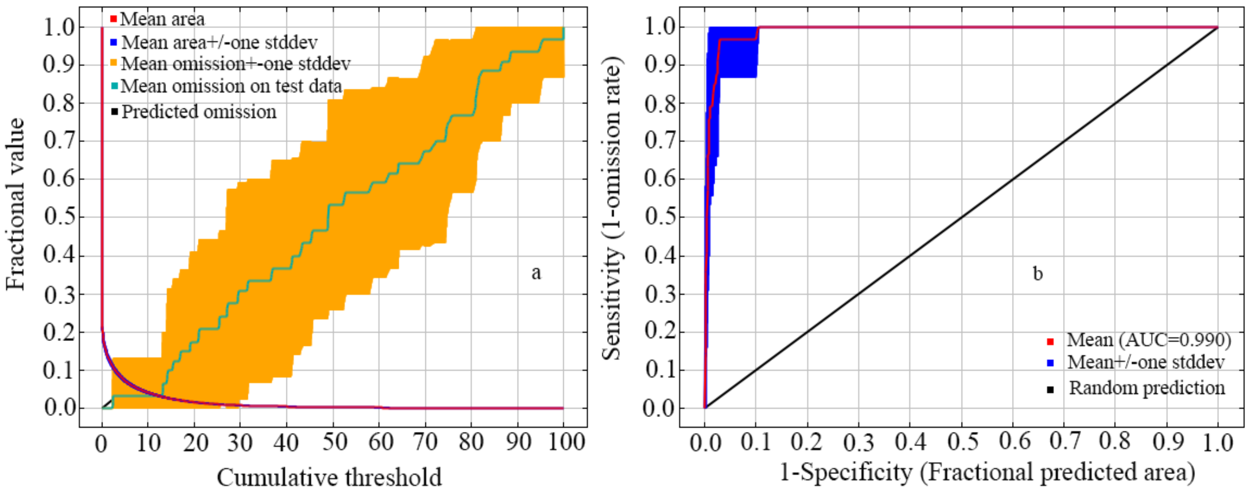

Figure 2. The validation of the model predicting *H. bodinieri* distribution: (**a**) omission rate; and (**b**) ROC curve.

3.2. Key Environmental Factors and Validating Modeling Results

Eight variables, after removing collinearity, were determined as key environmental variables affecting the potential distribution of *H. bodinieri*, according to the contributions to the MaxEnt modeling process by the jackknife test (Table 2). Of these, Bio18 (precipitation of the warmest quarter), Bio6 (minimum temperature of the coldest month), and Bio2 (mean diurnal range) had the highest contributions of 32.7%, 26.3%, and 20.5%, respectively (total contribution exceeding 79.5%; Table 2). Meanwhile, Bio6 (75.7%), Bio2 (13%), and Bio18 (6.9%) had the highest permutation importance values (Table 2). Therefore, these three bioclimatic factors (Bio18, Bio6, Bio2) were the main drivers of the modern geographical distribution of *H. bodinieri*.

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

Code	Bioclimatic Variable	Percent Contribution	Permutation Importance
Bio18	Precipitation of the warmest quarter	32.7	6.9
Bio6	Minimum temperature of the coldest month	26.3	75.7
Bio2	Mean diurnal range	20.5	13
Bio15	Precipitation seasonality	8.4	2.1
Bio4	Temperature seasonality	7.7	0.3
Bio14	Precipitation of the driest month	3.1	1.3
Bio13	Precipitation of the wettest month	0.9	0.4
Bio10	Mean temperature of the warmest quarter	0.4	0.2

Bio6 demonstrated the highest gain in regularized training and testing. Bio18 had the highest gain in AUC, indicating its leading contribution to the distribution of *H. bodinieri* (Figure 3). Bio2 and Bio13 had secondary contributions to the *H. bodinieri* distribution under the three gain patterns. In contrast, Bio10 had the lowest gain and the least importance, with little effect on predicting species distribution (Figure 3). The results showed that temperature exerted a greater effect on *H. bodinieri* distribution than precipitation (Figure 3, Table 2).

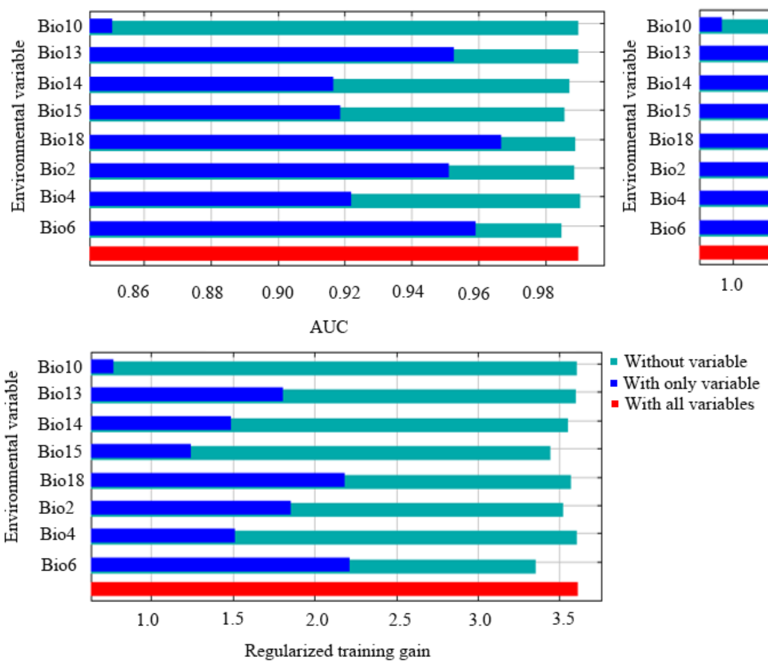

Figure 3. The relative predictive powers of the eight environmental variables based on the jackknife test of regularized training gain, test gain, and area under the curve (AUC) in MaxEnt.

The response curves built by MaxEnt between environmental variables and the probability of species presence indicated the influence of environmental stresses on the target species occurrence (Figure 4). Bio2, Bio4, Bio6, Bio10, Bio15, and Bio18 showed single-peaked curves, indicating that *H. bodinieri* had significantly adapted to these environmental variables. The response curves of Bio6 (minimum temperature of the coldest month) and Bio18 (precipitation in the wettest quarter) illustrated the effect of changing bioclimatic values on the distribution probability of *H. bodinieri* (Figure 4). Below −5 °C, the distribution probability was almost zero, and the suitable range of the minimum temperature of the coldest month (Bio6) for *H. bodinieri* was 2–5 °C. This result provides a strong basis for defining the extreme temperature range of *H. bodinieri* during winter in China. Moreover, when the precipitation in the wettest quarter (Bio18) was 580–720 mm, the distribution probability of *H. bodinieri* reached a peak. This result indicates the most suitable rainfall amount and temperature for its survival (Figure 4).

3.3. Predicting the Suitable Habitat of H. Bodinieri in China

The potential suitable distribution of *H. bodinieri* predicted by MaxEnt showed that the suitable area for the present climatic conditions is mainly located in the Southwest China provinces of Sichuan, Guizhou, Yunnan, Guangxi, and Guangdong (Figure 5). By habitat suitability, the total areas for the fail, poor, fair, good, and excellent suitability were 116.4×10^4 km^2, 8.35×10^4 km^2, 3.22×10^4 km^2, 1.85×10^4 km^2, and 1.93×10^4 km^2, respectively, comprising 12.13%, 0.87%, 0.34%, 0.19%, and 0.20% of China's total land area (960×10^4 km^2) (Table 3). Guangxi and Guizhou provinces had relatively large areas with excellent suitability at 1.19×10^4 km^2 and 0.71×10^4 km^2 (Table 3). Notably, the size of the current potential distribution is significantly larger than the present occurrence of *H. bodinieri* in China.

Table 3. Predicted suitable areas for *H. bodinieri* under the current climate in various provinces or autonomous regions (10^4 km^2). The ratio denotes the predicted suitable area divided by the total land area of the respective province or autonomous.

Province or Autonomous Region	Predicted Suitable Area Ratio				
	Fail	Poor	Fair	Good	Excellent
Guangxi	15.87	2.10	1.15	0.50	1.19
Guizhou	10.99	1.92	1.11	1.22	0.71
Guangdong	14.72	0.64	0.06	0.05	0.03
Sichuan	42.42	2.29	0.63	0.06	0.00
Yunnan	32.40	1.40	0.27	0.02	0.00
Total	116.4	8.35	3.22	1.85	1.93

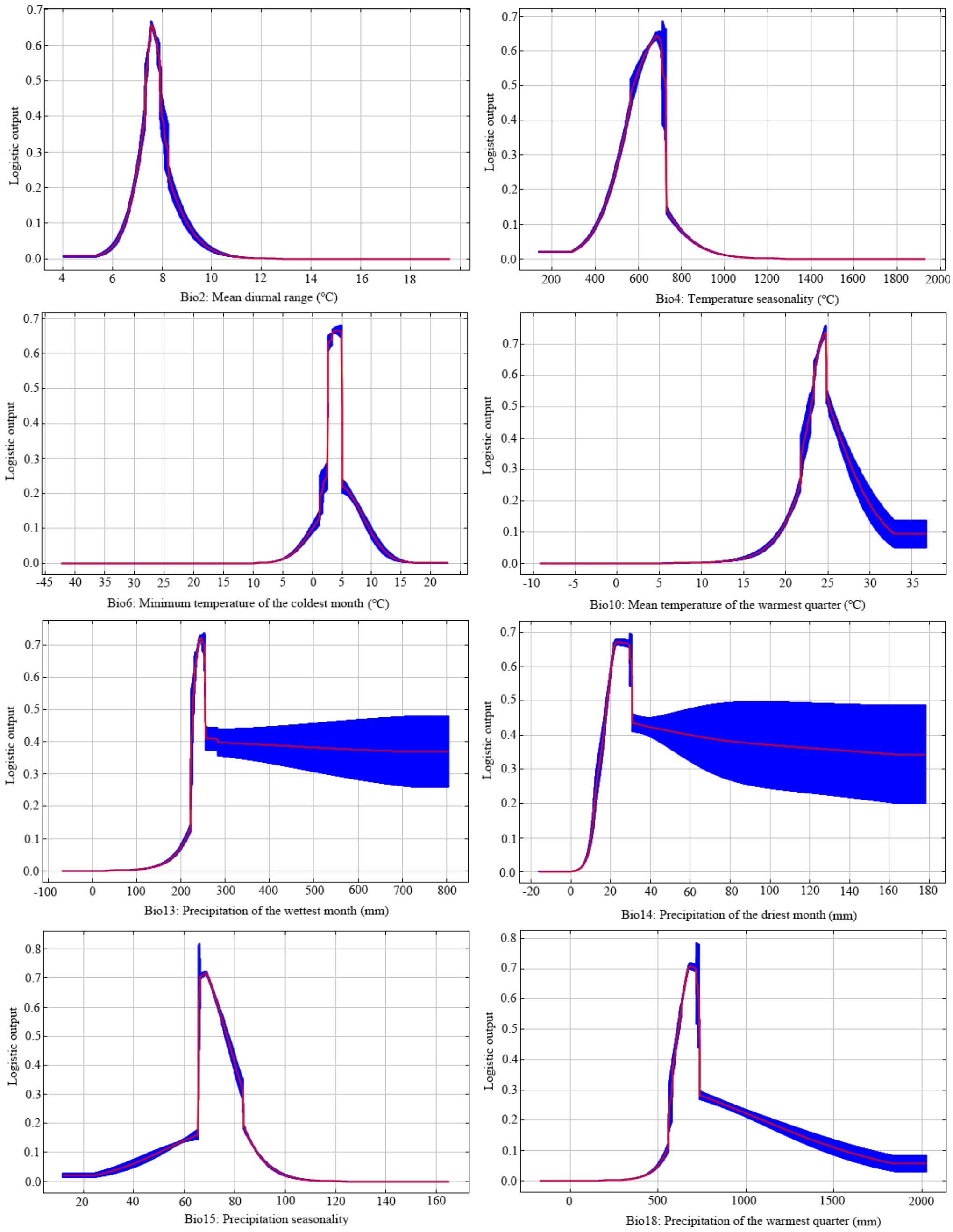

Figure 4. Response curves of the environmental variables to distribution probability.

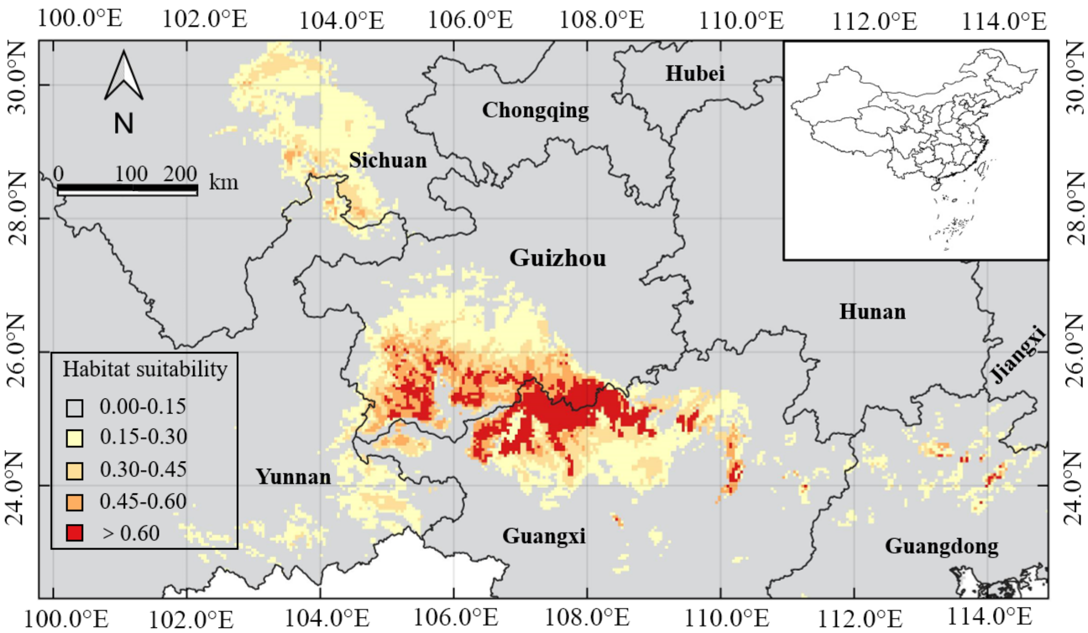

Figure 5. The predicted *H. bodinieri* distribution range obtained by MaxEnt modeling.

4. Discussion

The response relationship between species distribution and environmental factors is one of the important research topics in ecology to predict the species' geographical distributions and abundance distribution patterns [2,43]. This study was the first to explore the impacts of climate change on the geographical range and environmental suitability of the habitat of *H. bodinieri* in China using MaxEnt modeling. In this work, 44 valid occurrence records were used to conduct the analysis (Figure 1), which effectively solved the overfitting phenomenon in small samples and ensured the accuracy and stability of the simulation. Eight key environmental factors were chosen based on the contribution rate of each factor to the MaxEnt (Table 2). The final threshold-independent AUC reached 0.99 (Figure 2b), indicating that the MaxEnt predicted a high degree of fit between the habitat range and the actual suitable habitat of *H. bodinieri*. The results also demonstrated that MaxEnt could avoid overfitting and achieve a good prediction of species distribution areas despite a small sample size. It could provide an effective tool to protect and manage endangered species with an extremely small population [44].

The climate offers the most important factors shaping the physical geography of habitats and species distribution [45]. This main factor influences changes in constituent factors such as annual average temperature, extreme temperature, and annual average precipitation. Such changes can lead to the loss and fragmentation of species' habitats, seriously threatening endangered species with confined natural distribution and increasing their extinction risk [1,46].

Our results identified Bio18 (precipitation of the warmest quarter) as the main factor molding the potential distribution of *H. bodinieri*. The results pinpointed 580–720 mm as the most suitable range for precipitation of the warmest quarter (Figure 4), which may be related to the physiological characteristics of *H. bodinieri*. Based on existing distribution data, this endangered plant is mainly found in karst habitats with deficient surface runoff and sporadic occurrences of small soil pockets interspersed among many rock outcrops [47]. On fine and hot summer days, the strong sunshine vaporizes a large amount of soil water. Therefore, plenty of water is needed in the warm season to meet transpiration consumption and maintain normal physiology in such fragmented and harsh karst habitats.

Moreover, June to August is a critical period for ripening *H. bodinieri* fruits and seeds [48]. The higher precipitation of the warmest quarter benefits plant growth and development. It can also raise atmospheric humidity and soil moisture content to foster fruit growth and maturation and improve seed quality [49,50]. Proper seed development is critical for the species' reproductive prospects. If the seeds fail to mature, it will depress the population's natural regeneration ability, reducing species distribution and diffusion to exacerbate the population's decline.

Temperature substantially determines plant life activities and biochemical processes and plays an important role in shaping plant distribution [51,52]. Temperature can expand the plant's adaptability amplitude to habitat conditions and environmental changes within a certain range [37]. However, when a given temperature peak is exceeded, the habitat range shrinks or disappears [53]. The optimum minimum temperature of the coldest month (Bio6) is about 2–5 °C, indicating that the growth and development of *H. bodinieri* demand a certain heat level. Other studies showed that temperature could significantly favor the dormancy release of seeds, and appropriately low temperatures in the coldest month can break seed dormancy and promote subsequent germination [54]. Nevertheless, too low a temperature can cause injurious freezing, frost damage, and even inactivation of seeds [55], thus trimming the viable seeds for subsequent germination.

Our results predicted the potential distribution area that *H. bodinieri* may disseminate and spread in China beyond its current range (Figures 1 and 5). The spatial discrepancy between actual and potential ranges might be related to the limited scope of current research on *H. bodinieri*, focusing on biological characteristics [30,33]. Moreover, research data that accurately describe species' environmental requirements are scarce. Most individuals of *H. bodinieri* are distributed in disjointed, harsh, and mountainous karst habitats with largely inaccessible terrain. Therefore, it is difficult to acquire reliable and representative data to assess this endangered species' actual distribution area accurately. On the other hand, MaxEnt has the inherent trait of evaluating only niche-based species presence data. The model predicts the species' fundamental niche rather than the realized niche, which may result in overestimation [56,57]. Furthermore, predicting species distribution requires the consideration of physiological constraints, response to external factors and drivers, and competition in ecological communities. As it takes time for such factors to take effect, species' actual geographical distribution may lag behind climate change [58].

Notwithstanding, this species has thus far failed to colonize a larger extent of its suitable areas. This inability could be explained by extrinsic factors, including soil quality unsuitability, soil spatial discontinuity, interspecific competition, geographical barriers, human disturbance, and other unfavorable or stressful habitat conditions [59]. The lack of sufficient field data was one of the reasons for conducting this study. The results showed that the suitability area of *H. bodinieri* was only 7×10^4 km^2 (Table 3), mainly distributed in the Guangxi and Guizhou provinces, indicating a geographically confined suitability area.

The narrow spatial distribution is also related to the innate biological characteristics of *H. bodinieri* fruits. The fruits have a relatively large size that is difficult to spread over a long distance by wind. Most fruits randomly fall on microhabitats around the mother tree after ripening, creating a strong density dependence effect. Moreover, the fruits contain a large amount of oil, commonly consumed by rodents and other wildlife after falling to the ground [31]. In addition, the excessive collection of seeds by humans for oil and food has contributed to population decline [30]. The heavy natural seed predation and human harvesting have jointly curtailed the soil seed bank and seeds for subsequent germination. Such constraints demand more stringent requirements to protect and expand the range of *H. bodinieri*. Other studies have shown that the constricted spatial spread of rare and endangered plants is usually attributed to dispersal limitations and demographic stochasticity [60,61]. The resulting short-range dispersal distance can bring spatial aggregation [61]. Aggregated distribution may lead to patchy and mosaic distribution on the spatial scale and intensify competition among individuals of the species for limited environmental resources [47]. In sum, the combined consequences of the low reproductive survival rate and deleterious human activities have notably shrunk its distribution area and population size.

Our analysis identified suitable habitats for the ex situ conservation of *H. bodinieri*, providing a critical basis to protect its potential habitat. The distribution area, mainly the karst mountain region, denotes a unique landform that can provide relatively safe refuges for *H. bodinieri* to adapt more effectively to or survive the intensifying looming climate change. However, the spatial distribution of plants is influenced by abiotic and biotic environments, such as temperature, precipitation, altitude, presence of predators, human disturbance, geographic barriers, soil and vegetation type, etc. [62]. Especially after prolonged human interference, many suitable habitats have been eliminated, accompanied by altered forest land use. Moreover, past herbarium distribution records are not from the same year, and recent surveys are absent. Therefore, it is necessary to investigate the endangered plant's distribution status in detail and combine different biotic and abiotic factors to predict climate change's impacts on its distribution [7].

Some measures can be implemented to sustain and expand the range of *H. bodinieri*. They entail conducting deeper cognate studies to expand the knowledge base and translate research findings to enhance conservation practice. They include crucial issues such as the potential distribution of pollinators and seed dispersers, expanding existing nature reserves and protecting the surrounding habitat of the existing community, research on the impact of climate change on ecological relationships between this endangered plant and the surrounding associated trees [56], establishing new protected areas in high-risk regions in the context of climate change, protecting existing fruiting mother trees, and increasing viable seed sources to foster the reproduction and production of offspring. The areas predicted to be suitable but currently not occupied by the species offer candidate sites for prioritized conservation and propagation. It is necessary to strengthen habitat protection further and raise public awareness. Protection policies can be reinforced to reduce human impacts and implement ex situ protection. More comprehensive and accurate spatial data can be acquired to refine the *H. bodinieri* habitat distribution simulation.

5. Conclusions

The suitable areas of *H. bodinieri* in China were predicted by MaxEnt modeling, generating excellent outcomes with high accuracy. The highly suitable habitats for this plant were found primarily in China's Sichuan, Guizhou, Yunnan, Guangxi, and Guangdong provinces. The key environmental variables regulating its distribution are the precipitation of the warmest quarter (Bio18) and minimum temperature of the coldest month (Bio6), with the optimal conditions at 2–5 °C and 580–720 mm, respectively. These results help us to pinpoint the specific conditions for the optimal growth of the species and provide the scientific basis to improve the management and conservation of this endangered species.

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