



Habitat suitability modeling of a nearly extinct rosewood species (*Dalbergia odorifera*) under current, and future climate conditions

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Received: 14 December 2024 / Accepted: 18 February 2025 / Published online: 2 May 2025
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Abstract The influence of global climate change on endangered species is of growing concern, especially for rosewood species that are in urgent need of protection and restoration. Ecological niche models are commonly used to evaluate probable species' distribution under climate change and contribute to decision-making to define efficient management strategies. A model was developed to forecast which habitat was most likely appropriate for the *Dalbergia odorifera*. We screened the main climatic variables that describe the current geographic distribution of the species based on maximum entropy modelling (Maxent). We subsequently assessed its potential future distribution under moderate (RCP_{2.6}) and severe (RCP_{8.5}) climate change scenarios

for the years 2050 and 2070. The precipitation ranges of the wettest month and the warmest quarter are the primary limiting factors for the current distribution of *D. odorifera* among the climatic predictors. Climate change will be expected to have beneficial effects on the distribution range of *D. odorifera*. In conclusion, the main limits for the distribution of *D. odorifera* are determined by the level of precipitation and human activities. The results of this study indicate that the coasts of southern China and Chongqing will play a key role in the protection and restoration of *D. odorifera* in the future.

Keywords Climate change · *Dalbergia odorifera* · Habitat suitability · Model tuning · Forest conservation

Project funding: This work is funded by the National Natural Science Foundation of China (NSFC 31761143002, NSFC 3207178), China Postdoctoral Science Foundation (2022M710405), and the National Forest and Grassland Genetic Recourse (No. 2005DKA21003).

The online version is available at <https://link.springer.com/>.

Corresponding editor: Lei Yu.

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Introduction

Dalbergia odorifera T. Chen is a semi-deciduous rosewood species under state protection by the Chinese government (Wang and Xie 2004; The SN 2017). Rosewood is one of the most exploited tree species around the world, as it is used to produce luxurious furniture, and musical instruments, as well as valuable oil. *Dalbergia odorifera* is widely appreciated in Chinese furniture culture and is known for its medicinal properties, traditionally employed to address a range of health issues including blood disorders, necrosis, cardiovascular diseases, and diabetes (Wang and Xie 2004; Wariss et al. 2018). However, the growth rate of medicinal material and heartwood in *D. odorifera* is relatively slow (Cui et al. 2016), and it might take more than 100 years to maturity (Qin et al. 2022). These limitations to the availability of rosewood resources have led to high prices and cultivation, selective logging, and deforestation. According to the comprehensive survey conducted by Meng (2010), no more than 50 natural individual trees of *D. odorifera* were

found in Hainan province, China. *Dalbergia odorifera* is endemic to Hainan province but has been widely introduced and cultivated in other subtropical areas in China since the 1950s, such as Fujian (Yao et al. 2012), Zhejiang, Guangdong, Guangxi and Yunnan (Hong et al. 2020). After several decades of domestication, various experiments have yielded promising results. *D. odorifera* showed strong adaptability in Guangxi and was able to grow to the same height and diameter as in its indigenous area (Li 2012; Qin et al. 2023). However, some studies indicate that *D. odorifera* population growth is sensitive to soil conditions, such as soil porosity, pH value, Ferrum and Aluminum ionic contents (Dexter 2004). Our earlier study found the distribution of *Dalbergia cultrata* was primarily affected by temperature and precipitation patterns (Liu et al. 2019), the species is endemic to Yunnan province. Based on the limiting factors observed in closely related species and the finding that seed breeding is primarily influenced by temperature, we hypothesize that temperature and precipitation are the key natural factors affecting species distribution. But which one of thermal and rainfall conditions is still unclear and fully understood.

Climate change has become one of the major challenges as it is adding enormous pressure to species' survival and the integrity of ecosystems (Root et al. 2003). Climate influences species distribution ranges, physiological responses, and survival rates in different regions, as well as influences species redistributions (Raghavan et al. 2019; Lawlor et al. 2024). The significant threats posed by climate change to plant species encompass extinction due to habitat loss (Aguirre-Gutiérrez et al. 2017), and reduced viability resulting from range contraction (Thuiller et al. 2005). These factors are threatening in particular species that already have restricted distribution ranges because of their narrow environmental suitability (Thuiller et al. 2005; Divíšek et al. 2018). As multiple environmental factors are influencing biodiversity, with different intensities depending on the life cycle of the plant species (Urban et al. 2016), it is unlikely to consider all the factors when creating a model to estimate the current and future distribution of a species based on environmental predictor variables (Morris et al. 2020). Precipitation is caused by increased moisture convergence as a result of thermodynamic changes, which can also result in water vapor flow. Therefore, in order to accurately forecast the responses of endangered species to various climate scenarios, such as climate adaptation or extinction risk (Lenoir and Svenning 2015; Zhang et al. 2021), it is critical to identify the key variables. Such findings can be important and valuable contributions for scientists and farmers to formulate future monitoring and management strategies. Ecological niche models are commonly used to evaluate probable species distribution under climate change. MaxEnt exhibits strong data compatibility and delivers impressive predictive performance, which is popular in ecological

niche modeling (Behroozian et al. 2020; Zhao et al. 2022). Tian et al. (2012) systematically evaluated the capability of the CCSM4.0 model over East Asia and China and showed a reliable capability to simulate the large-scale climate features over East Asia and China. The CCSM4 has been used intensively in the context of paleoclimate modeling for the study of the mid-Pliocene (Feng et al. 2022), the most recent glacial cycle (Kageyama et al. 2021) and the mid-Holocene (Tiwari et al. 2023). Two major periods, the mid-Holocene and the Last Glacial Maximum are frequently used in climate studies (Bartlein et al. 2011). According to the report, the climate of the mid-Holocene scenario is warmer and wetter than the current, whereas the Last Glacial Maximum is cooler and drier. For example, the temperature is estimated to climb by an average of 2.7 °C by 2050–2070, whereas in the past it was 1.1 °C lower.

Dalbergia odorifera has always been used to make furniture and was highly prized during the Qing Dynasty (1644–1911). However, human activities have led to its decline over time. Historical distribution patterns cannot be verified, and the geographical and topographical aspects of its current distribution sites offer limited reference value. Today, the species is endangered and confined to Hainan Province, with its natural distribution no longer widespread. According to previous surveys, the wild population of *D. odorifera* faces severe threats from overexploitation and habitat loss (Meng et al. 2010; Liu et al. 2017). Although the species has been introduced to some provinces in China, it may require over forty years to reach full flowering and a century to mature for harvest (Qin et al. 2022). Few studies have evaluated the effects of climate change on *D. odorifera*. Therefore, we selected environmental factors to predict its suitable distribution areas, aiming to critically analyze the potential reasons for its projected range expansion and to understand the influence of different climatic variables. Using maximum entropy modeling (MaxEnt) based on occurrence data, our objectives were: (1) to identify key climatic variables that constrain and explain the distribution of *D. odorifera*; (2) to predict habitat suitability trends under various climate scenarios, and (3) to propose strategies for the conservation and restoration of *D. odorifera*.

Material and methods

Occurrence sources

A total of 156 occurrence records of *D. odorifera* were acquired from several sources. Of them, 90 records were obtained by field surveys in Hainan province in March 2018. These occurrence sites were mostly scattered in places with elevation ranging from 600 to 1400 m, between 18°41' N to 19°31' N latitude and 108°44' E to 109°20' E longitude.

Another 52 historical occurrence records (after 1950) were obtained from the database of the Chinese Virtual Herbarium (CVH, <http://www.cvh.org.cn/>), and the database of the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>). Specimens and observation records of *D. odorifera* were the results of these data, which were found in Changjiang, Ledong, Jianfengling, and Baisha. Furthermore, the literature provided 14 occurrence records (Meng et al. 2010).

Data processing

The train samples were selected by screening them for a certain number of years which were shown in the event of a proofreading and screening. Since the spatial resolution of the environmental variables is 2.5 arcminutes (approximately 5 km near the equator), when the distance between two occurrence records was less than 3 km, only one of them was retained (Wang et al. 2017). Using 2.5 arcminute resolution is regarded sufficient for SDM when comparing past, present, and future climate projections as it balances ecological relevance, computational efficiency, and consistency with the typically lower resolution of available climate models (Hijmans et al. 2005). So set the buffer radius to 1.5 km, and 3 km threshold for removing spatially clustered points. Finally, 129 occurrence records of *D. odorifera* were retained to model the suitability habitat. Among them, 90 records were derived from the field survey, 22 from CVH, 3 from GBIF, and 14 from other literature. (<https://www.inaturalist.org/observations/213424559>; <https://doi.org/10.15468/ab3s5x>; <https://doi.org/10.15468/rx4p4w>).

Environment and map data

Bioclimatic variables include the data of rainfall, the monthly temperature, which is used as the basis for environmental variables. A detailed description of the 20 environmental variables used in this study is presented in Table 1. The environmental variables for the baseline period (1960–1990) and three past periods (Mid Holocene-CCSM4, Last Glacial Maximum-CCSM4, Last inter-glacial) were downloaded from <http://www.worldclim.org>. To represent future climate conditions (2050 and 2070), we selected a well-simulated model (Liu et al. 2019) atmospheric circulation model (CCSM4) from the fifth IPCC report (IPCC 2018) under two emission scenarios (RCP_{2.6} and RCP_{8.5}) and two-time horizons (2050 and 2070). The *D. odorifera* was projected to past and future climatic conditions by modelled under baseline conditions.

Table 1 Bioclimatic variables and topographical factors

Variables and description	Unit
Bio1 = Annual Mean Temperature	°C
Bio2 = Mean Diurnal Range	°C
Bio3 = Isothermality	%
Bio4 = Temperature Seasonality	°C
Bio5 = Max Temperature of Warmest Month	°C
Bio6 = Min Temperature of Coldest Month	°C
Bio7 = Temperature Annual Range	°C
Bio8 = Mean Temperature of Wettest Quarter	°C
Bio9 = Mean Temperature of Driest Quarter	°C
Bio10 = Mean Temperature of Warmest Quarter	°C
Bio11 = Mean Temperature of Coldest Quarter	°C
Bio12 = Annual Precipitation	mm
Bio13 = Precipitation of Wettest Month	mm
Bio14 = Precipitation of Driest Month	mm
Bio15 = Precipitation Seasonality	%
Bio16 = Precipitation of Wettest Quarter	mm
Bio17 = Precipitation of Driest Quarter	mm
Bio18 = Precipitation of Warmest Quarter	mm
Bio19 = Precipitation of Coldest Quarter	Mm
Alt = Altitude	M

Variable selection

We deleted duplicate and highly correlated variables to increase the performance of the distribution models. First, we ran MaxEnt with all 20 environmental variables and eliminated those that did not contribute to the probable habitat distribution. Subsequently, we checked the cross-correlations (Pearson correlation coefficient, $r > 0.8$ or $r < -0.8$) of the remaining bioclimatic variables, obtained from the *D. odorifera* occurrence records (Dormann et al. 2013). Due to the correlation analysis and variable contributions, a part of the variables was kept for the MaxEnt analysis.

The cumulative contribution of variables was calculated to eliminate highly cross-related variables and improve the performance of the model (Table 2). The outcome indicated that there was no contribution from four bioclimatic variables (bio5, bio7, bio8, and bio19) and were removed. We also computed the Pearson correlation coefficient (r) for the remaining bioclimatic variables. When $r > 0.8$ or less than 0.8, pairwise variables are thought to have a significant association (Cotrina et al. 2021). Thereby, each highly correlated variable that contributed less to the model was eliminated (Bio 6, Bio15, Bio11, Bio16, Bio9, Bio17, Bio3, and Bio12). Bio14 was kept even though it was highly correlation with Bio4 ($r=0.908$) because it showed the highest permutation importance (31.3%). The correlation coefficient of pairwise variables were listed in Table 3. Ultimately, seven

Table 2 The cumulative contribution of each environmental variable to the probable distribution of *D.odorifera*

Environmental variables	Percentages of contribution (%)	Permutation importance (%)	Environmental variables	Percentages of contribution (%)	Permutation importance (%)
BIO13	32.10	7.90	BIO9	0.10	0.00
BIO4	18.10	12.60	BIO17	0.10	1.00
BIO18	12.50	4.40	BIO3	0.10	3.60
BIO2	11.40	13.00	BIO10	0.10	2.20
BIO1	8.80	16.90	BIO12	0.10	2.30
BIO14	7.50	31.30	BIO19	0.00	0.00
BIO6	4.80	1.30	BIO7	0.00	0.50
BIO15	4.00	1.20	BIO8	0.00	0.00
BIO11	0.20	1.80	BIO5	0.00	0.00
BIO16	0.20	0.10			

Table 3 Pair-wise Pearson's correlation coefficients of environmental variables.

Environmental Variables	BIO1	BIO2	BIO4	BIO10	BIO13	BIO14	BIO18
BIO1	1						
BIO2	−0.107	1					
BIO4	−0.676	−0.125	1				
BIO10	0.626	−0.345	0.147	1			
BIO13	−0.267	0.205	0.067	−0.321	1		
BIO14	−0.671	−0.015	0.908	0.049	0.309	1	
BIO18	−0.441	0.228	0.466	−0.155	0.708	0.587	1

environmental variables were chosen and then the MaxEnt model was repeated.

MaxEnt model

We examined the habitat suitability curves and calculated the contributions of each variable to the habitat model of *D. odorifera* using the software's built-in jackknife test, which was performed with ten repetitions (Hill et al. 2012). The evaluation of model performance was calculated using the AUC value, which serves as a crucial measure of the performance of the prediction model (Elith et al. 2006). In this study, the average AUC value of the fifty repetitions served as criteria to evaluate the model's performance. In general, the AUC should be between 0.5 and 1. If the value is less than 0.5, this indicates a pure guess. According to Yi et al. (2016), we classified the model performance according to the AUC value as fail (0.5–0.6) and excellent (0.9–1.0). The huge geographic extent that determines the AUC value from which background information is chosen can be used to inflate the AUC value. Therefore, two additional criteria, TSS and Kappa, were selected as evaluation criteria for the model (Lobo et al. 2008). The TSS and Kappa should be between 0 and 1, and we classified the model performance based on TSS and Kappa as poor (0.5–0.7), fair (0.7–0.8),

good (0.8–0.9), and excellent (0.9–1) (Fourcade et al. 2017). We ran random splitting for model training before testing.

After running the MaxEnt model, the export file was imported in ArcGIS and the *.ASCII files were converted to *.Raster file. The equidistance classification of Spatial Analyst Tools was used to reclassify the grades of habitat suitability. The results were combined with the vector layer of the global country-level boundaries (REF) to produce the maps (Fig. 1).

Results

Variable's contributions and model performance

As shown in Fig. 2, the estimated ROC indicated that the dataset had an average AUC of 0.991, a TSS value of 0.925, and a Kappa value of 0.909, which indicated good model performance. Figure 3 displays the contribution to the habitat distribution of seven variables that were computed using the jackknife test. High grains from Bio13 and Bio18 (>1.5, independently), suggesting that the most helpful information is contained in these variables. Bio14 had the lowest gain among the variables when used independently and is therefore likely to hold little useful information.

Fig. 1 The occurrence records of *Dalbergia odorifera*

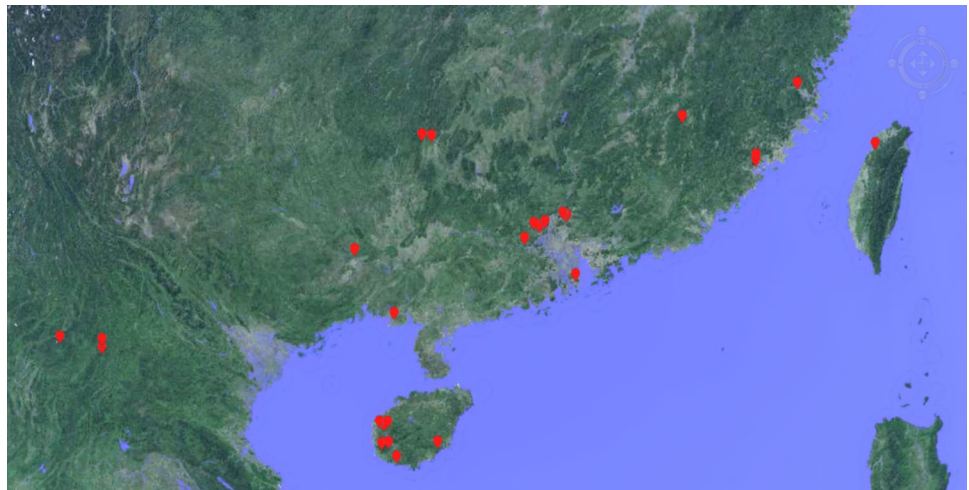
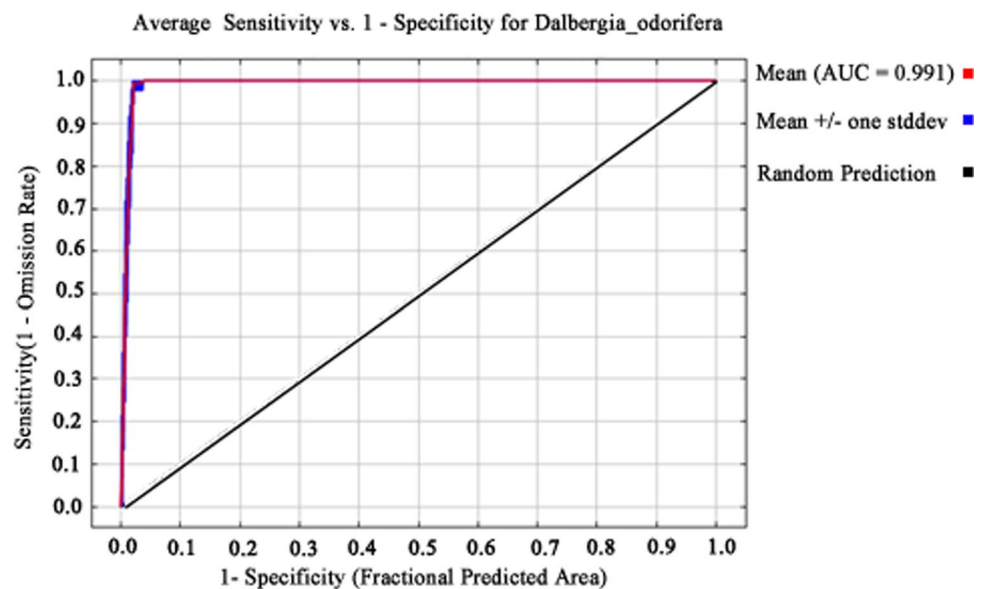


Fig. 2 The results of AUC curves. (The blue line (testing) indicates the fit of the model to the testing data/ The red line (training) indicates the “fit” of the model to the training data)



Future scenarios of climate change

The probable habitat distribution of *D. odorifera* was reclassified into four categories, based on equal interval classification: (1) habitat not suitable ($P < 0.15$); (2) habitat of low suitability ($0.15 < P < 0.40$); (3) habitat of normal suitability ($0.40 < P < 0.70$); (4) and habitat of high suitability ($0.70 < P < 1.00$). The probable distribution in Southeast Asia is shown in Fig. 4. The model showed that the tropical zones in Asia Pacific Rim, northern Vietnam, and the southern coast of China have good environmental conditions ($P > 0.7$) for *D. odorifera* (14° N– 26° N; 94° E– 112° E). The most valuable climatic features of *D. odorifera* were periodic changes in precipitation intensity and temperature seasonality. Areas in southwestern and northern Bangladesh, southeastern Nepal, and Chongqing in China were predicted as moderately suitable areas. A total of 3,030,000 km² was

estimated to be the range of *D. odorifera* potentially suitable areas. Approximately ~424,000 km² (~14.0% of the total) was projected as high suitability, and ~725,000 km² (~23.9%) showed moderate suitability (Fig. 3).

Limiting environmental factors that affect the species' distribution

According to the response curves, there is a correction between environmental variables and the appropriateness of the environment, which shows that the species has a different ecological niche. The ranges of suitability for environmental variables were found by the threshold of medium suitability, with an average logical value of 0.47. The response curves of seven variables to the habitat suitability of *D. odorifera* are shown in Fig. 5, and the suitable range of each variable

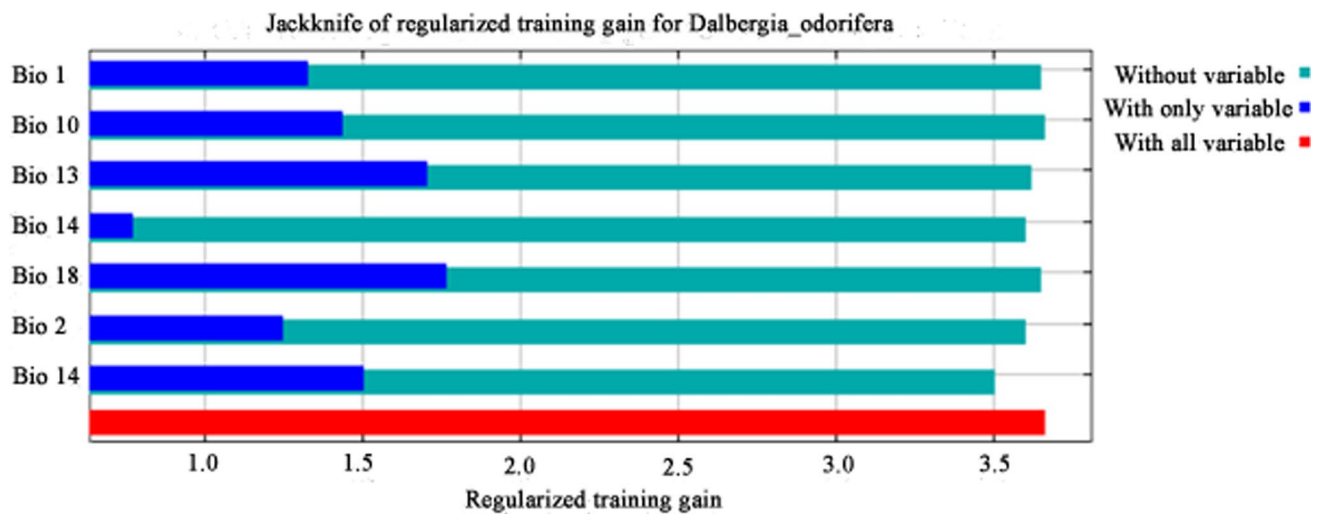


Fig. 3 The results of the jackknife test of variables' contribution in *Dalbergia odorifera*'s model. (The regularized training gain describes how much better the MaxEnt distribution fits the presence data compared to a uniform distribution. The blue bars represent the gain from

using each variable in isolation, the green bars represent the gain lost by removing the single variable from the full model, and the red bar represents the gain using all of the variables)

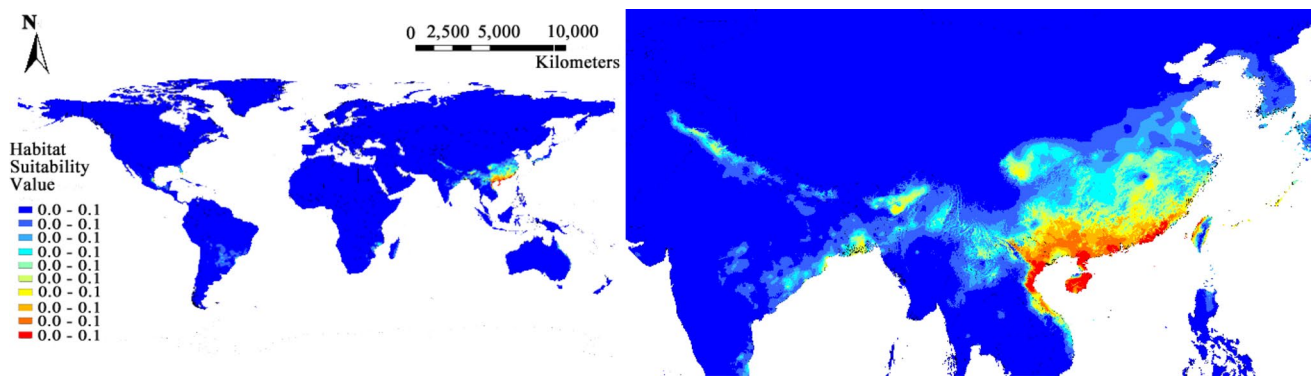


Fig. 4 Probable distribution of *Dalbergia odorifera*

is listed in Table 4. The important climatic factors associated with the suitable range was 212–356 mm for precipitation of the wettest month, with optimal precipitation of 270.34 mm; the suitable range for mean temperature of the warmest quarter was 281.04–597.11 mm, with an optimum value of 337.77; and the suitable range for precipitation of warmest quarter was 369.23–1434.89 mm, with the optimum precipitation of 567.85 mm; the suitable range for mean diurnal range was from 5.9 to 7.5 °C, with optimum annual mean temperature of 24.3 °C.

Compared to the current model extent, the probable distribution area amounted to ~2,980,000 km² (decrease of 1.48%) based on RCP_{2.6}-2050 (Table 5) and to ~2,990,000 km² (decrease of 1.48%) under RCP_{2.6}-2070. The potential distribution area amounted to ~3,400,000 km² (decrease of 1.24%) under RCP_{8.5}-2050 (increase of 12.13%), and to ~3,180,000 km² based on RCP_{8.5}-2070 (increase of 5%).

In addition, under the RCP_{8.5} and RCP_{2.6} situations, the highly-potential distribution areas are increasing both. The highly suitable areas were expanded to Southern Laos from Vietnam and small areas in Northern Bangladesh. Under the RCP_{2.6}-2050 scenario, the highly suitable areas amount to ~434,000 km² with an increase of 2.33% compared to the current climate condition, and more widely distributed throughout Vietnam; the areas were further expanded under the RCP_{2.6}-2070 condition, with a 4.83% increased. Under the RCP_{8.5}-2050 and RCP_{8.5}-2070 scenarios, highly suitable areas were forecasted to be more distributed in Chongqing province, with an increase of 3.84 and 4.48%, respectively.

Under four simulated situations, more areas are turning out to be moderately suitable. The area growth rates of all scenarios exceeded 10 per cent compared to the current climate condition. Under RCP_{8.5} (2050 and 2070) scenarios, the increase in expanding area exceeds 30% (Table 5).

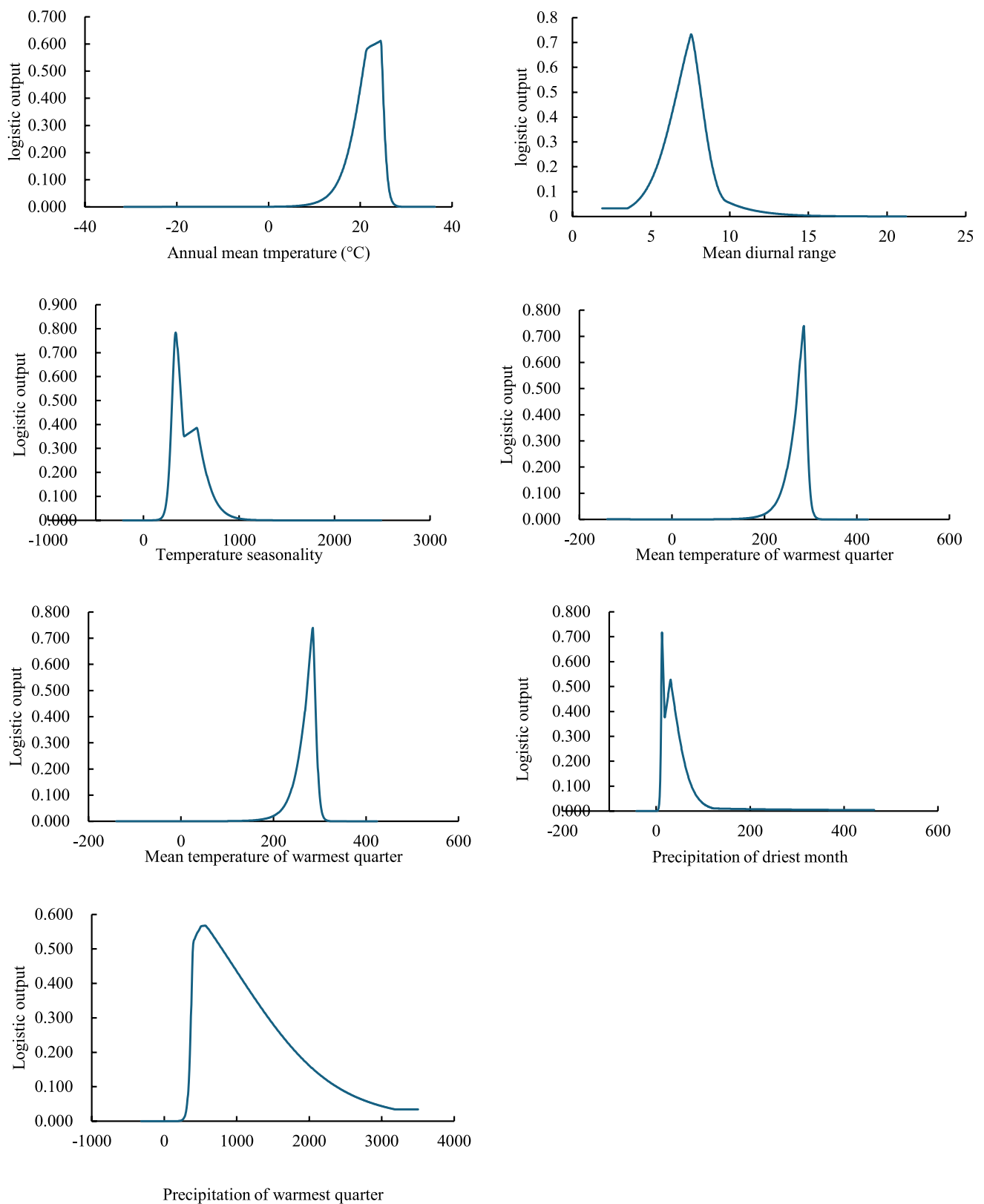


Fig. 5 Response curves of seven environmental variables in *Dalbergia odorifera* distribution model

Table 4 The range of environmental variables affecting the probable distribution of *Dalbergia odorifera*

Environmental variables	Range	Optimum value
BIO18: Precipitation of Warmest Quarter (mm)	369–1435	568
BIO4: Temperature Seasonality (°C)	281–597.1	337.8
BIO13: Precipitation of Wettest Month (mm)	212–356	270
Bio2: Mean Diurnal Range (°C)	5.9–8.6	7.5
Bio14: Precipitation of Driest Month (mm)	10–49	13
Bio10: Mean Temperature of Warmest Quarter (°C)	25–29.4	28.5
BIO1: Annual Mean Temperature (°C)	18.5–25.1	24.5

Table 5 Predicted suitable areas worldwide for *Dalbergia odorifera* in globe under current and future climatic conditions (km²)

Species	Classification level	Current climate	Future climate conditions			
			RCP2.6–2050	RCP8.5–2050	RCP2.6–2070	RCP8.5–2070
<i>Dalbergia odorifera</i>	Suitable habitat (0.05–1)	~3,030,000	~2,980,000 (1.48%)	~3,390,000 (12.13%)	~2,990,000 (1.23%)	~3,180,000 (5.0%)
	Low habitat suitability (0.05–0.18)	~1,880,000	~1,690,000 (−9.75%)	~1,990,000 (6.0%)	~1,740,000 (−7.19%)	~1,770,000 (−5.47%)
	Moderate habitat suitability (0.18–0.37)	~725,000	~854,000 (17.71%)	~964,000 (32.89%)	~803,000 (10.64%)	~960,000 (32.30%)
	High habitat suitability (0.37–0.75)	~424,000	~434,000 (2.33%)	~441,000 (3.84%)	~445,000 (4.83%)	~443,000 (4.47%)

Overall, the entire suitable habitat areas under climate change do not make sense to the current situation. However, the moderate and highly suitable areas of *D. odorifera* will increase under climate change, such as Chongqing in China, Northeastern Bangladesh, and Southern Laos. The introduced individuals of *D. odorifera* showed high germination ability and produced new viable generations at optimal temperatures. Therefore, we strongly recommend additional measures to expand the narrowed distribution range of the species through introduction also in moderately suitable habitats, such as Chongqing and Northern Bangladesh.

Discussion

Modeling response and habitat suitability

An ecological niche model was created for *D. odorifera* using MaxEnt to analyze the change of probably suitable habitat through time and space. Efficient input data (e.g., accurate occurrence data and up-to-date environmental variables) can optimize the predictive capacity of the model (Ashcroft et al. 2011), and the selection of the variables has a remarkable effect on the resulting species distributing model (Jiang and Ma 2014). The Pearson correlation analysis and a partial ROC evaluation were used to determine the model, which was regarded as trustworthy and performed well (Acevedo et al. 2012). The jackknife test from MaxEnt showed that Bio13

(Precipitation of Wettest Month) and Bio18 (Precipitation of Warmest Quarter) have the highest contributions to this model, and the response curve indicated that precipitation has a strong effect on the distribution of the species. Meng et al. (2010) suspected temperature and humidity as the main factors of plantation success of *D. odorifera*. Temperature (Bio1, Bio2, Bio4, Bio10) also played a significant role in the distribution model of the species in this study. According to life-table studies, the annual mean temperature range for this species was determined to be between 18.5 °C and 25.1 °C, which aligns with the findings of Meng et al. (2010), who noted an optimum range of 17.3 °C to 28.8 °C. The main factors were different from our previous study of *D. culturata*, which showed the primary importance of temperature fluctuation (Liu et al. 2019).

Increasing highly distribution areas under climate change

The results of our study indicate a considerable increase in moderate and highly suitable areas for *D. odorifera*, under future climate conditions in 2050 and 2070, which support the idea that climate change will significantly impact the shifts of species distribution (Thomas et al. 2004). *D. odorifera* has expanded to Guangxi, Guangdong, and Fujian provinces due to introduction and conservation (Meng et al. 2010; Liu et al. 2017). In our study that Bangladesh, North India, Laos, Vietnam, and Chongqing may provide suitable

habitats for *D. odorifera*. These sites provide us with the direction of introduction and trial planting. Even though the total area of suitable habitat is predicted to remain stable with global warming, we predicted an increase in moderately and highly suitable habitat for *D. odorifera*. The species that are sensitive to temperature may be moving to cooler regions at higher latitudes or altitudes (Tang et al. 2018). Under the future model, *D. odorifera* could expand to specific areas, such as North India and Chongqing, showing the complexity of the limitation of the species' distribution.

Threats to the species

Thermodynamic changes mainly reflect the enhanced water-holding capacity of the atmosphere in the south, which lead to increased moisture convergence and thus wetting (Tian et al. 2018). The weakened southerly flow results in less water vapor reaching far to the north and thus reducing precipitation there (Li et al. 2018; Zhou et al. 2020). In general, climatic warming has its advantages and disadvantage for different plant species in various locations. Beneficially, elevated CO₂ and temperature can improve the plants' photosynthesis ability in the short term (Poorter and Navas 2003). Nonetheless, certain studies have suggested that increased temperatures and higher CO₂ levels may produce negative impact on plants, for instance, warming has been shown to decrease flower counts and seed production in some species (Liu et al. 2012). Increasing frequency and intensity of extreme weather conditions is considered to be one of the key risks for plants in tropical areas in Asia, e.g., long-term and large-scale droughts and floods, etc. (Jiang and Ma 2014). Too much dryness or hydrops might threaten the survival and distribution of *D. odorifera*. The anticipated range contraction of *D. odorifera* in this study can provide insights into conservation and plantation strategies. Species distribution modeling considers climatic and geographic factors. Nevertheless, human activity, species adaptability, and interspecies competition might affect the distribution of species (Cauwer et al. 2014). In the event that we took into account every one of the risks, areas with a high suitability for *D. odorifera* are probably much smaller than the anticipated results. From our knowledge, the wild population of *D. odorifera* decreased rapidly in the last decade due to overharvesting and changing land use management. In 2010, natural populations of *D. odorifera* counted not more than hundred individual trees in Hainan Island in China (Meng et al. 2010).

Protection and recovery strategy of the species

With global warming over dozen decades, the precipitation of the monsoons has changed dramatically and had a significant effect on plants (Zhou et al. 2008; Liu et al. 2009; Hsu et al.

2012). Moles et al. (2014) regarded that the mean annual temperature is better predictor than mean yearly precipitation. But according to Zhao et al. (2018), temperature and precipitation showed the same impact on the distribution of plant species. We were able to prove this in our previous study of *D. cultrata* (Liu et al. 2019) as well as in this study of *D. odorifera*.

However, analyzing long-term spatial and temporal variations, we found different influencing factors regarding the probable distribution of *D. odorifera*. Compared with the mid-Holocene situation, *D. odorifera* had similar possible distribution areas as in the present (Supplementary Fig. 2). However, under the last Glacial Maximum scenario, the probable distribution areas of *D. odorifera* were significantly larger than now and the species was found in central Africa (Supplementary Fig. 3). This result indicated that the probable geographic distribution of *D. odorifera* had been influenced by a major reduction of mean diurnal range and annual mean temperature over an extended period of time and it is now predicted to slightly change over the next 30 or 50 years, resulting in a slight expansion. Although the species is listed in the IUCN Red List as 'vulnerable' and it is under a certain type of protection (Yu et al. 2017), human activities such as logging are probably still the most serious threat to this species. The resulting small population and fragmentation make the species more vulnerable and less resilient to climate change stresses (Behroozian et al. 2020). Moreover, conservation-oriented restoration in highly suitable areas should be considered for species restoration (Volis 2017, 2019). However, systematic research on *D. odorifera* is slow, so it is necessary to increase the number of studies on the conservation biology of *D. odorifera* to improve its conservation status significantly. It could be considered to introduce to areas with a large temperature difference between day and night rather than only within the historical distribution, such as south part of Zhejiang, meanwhile, the study on seed germination and seedling growth under temperature gradient threat. This could better understand how the species adapt to temperature changes and find the mechanism of its resistance ability. Observing the process of adaptive evolution of this species may help to predict the true distribution of this species under the conditions of past and future environmental changes.

Limitations

Earlier studies showed that MaxEnt models performed better than other models when the sample sizes were small (Schmidt et al. 2020; Zeng et al. 2016; Wei et al. 2018). There are still certain drawbacks to the *D. odorifera* model, even if it performed well. Firstly, species' probable distributions are affected by human activity (e.g., because of logging and plantation of other species), which narrows the species' suitable habitat. Additionally, only small populations of this species

could be found, in particular wild populations. The occurrence data of well-cultivated populations were added to the analysis of the model (Meng et al. 2010), which might have led to an overestimation of the potential areas. Some studies also suggest the extent of the study areas might influence the results of the validation of the final model (Elith et al. 2011); for example, model performance could be improved by controlling the selection of the study area (Barbet-Massin et al. 2012). Furthermore, this study focused solely on climate variables, overlooking other important factors that affect species distribution, such as niche competition (both intraspecific and interspecific) and topography (including aspect and slope). Therefore, with wider introduction and plantation in the future, more elements should be taken into consideration. Future modelling analyses should also include considerations on land use, probable policy change, as well as different threats deriving from human activities.

Conclusion

Based on occurrence data and specific environmental information at the global level, the probable spatial distribution of *D. odorifera* was predicted. This species is sensitive to precipitation and temperature fluctuation. The annual temperature range and precipitation are the primary characteristics that limit the distribution of *D. odorifera*. However, the results show that the highly suitable habitat of *D. odorifera* is likely to increase in certain areas under projected climate change. Climate warming may be beneficial for the species to some extent, but there are major conservation concerns regarding illegal logging and extreme weather events. The probable distribution maps of *D. odorifera* which include habitat suitability classes will be useful for creating new protected areas and identifying sites for species introduction and habitat restoration.

Acknowledgements Thanks to Fritz kleinschroth who provided manuscript reading, and many thanks to Fidel Chiriboga for helping analyze teaching during the research. Thanks to CVH (<http://www.cvh.org.cn/>) and GBIF (<https://www.gbif.org>) for providing the records of *D. odorifera* and records of distribution maps.

Funding This work is funded by the National Natural Science Foundation of China (NSFC 31761143002, NSFC 3207178) China. Post-doctoral Science Foundation (2022M710405) and the National Forest and Grassland Genetic Recourse (No. 2005DKA21003). The online version is available at <https://link.springer.com/>

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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