forests

Article

MaxEnt Modeling for Predicting Suitable Habitat for Endangered Tree *Keteleeria davidiana* (Pinaceae) in China

Qin Zhang [1], Xiangbao Shen [1,2], Xiaolong Jiang [1], Tingting Fan [1], Xiaocui Liang [2,3,4,5,*] and Wende Yan [2,3,4,5,*]

1 The Laboratory of Forestry Genetics, Central South University of Forestry & Technology, Changsha 410004, China
2 National Engineering Laboratory for Applied Technology of Forestry & Ecology in South China, Changsha 410004, China
3 Faculty of Life Science and Technology, Central South University of Forestry & Technology, Changsha 410004, China
4 Lutou National Station for Scientific Observation and Research of Forest Ecosystem, Yueyang 414000, China
5 Key Laboratory of Subtropical Forest Ecology of Hunan Province, Changsha 410004, China
* Correspondence: t20081388@csuft.edu.cn (X.L.); t20001421@csuft.edu.cn (W.Y.)

Abstract: Understanding species response to climate change is essential for the conservation and utilization of species resources under rapid climate change in the future. In this study, the present and future suitable distribution range of *Keteleeria davidiana*, a tertiary relict gymnosperm, was predicted based on the maximum entropy model (MaxEnt). A total of 158 occurrence records were collected after removing the duplicated records. Six low-correlation climate variables were used to predict species distributions. The three key climate factors that affect the distribution of *K. davidiana* were temperature seasonality (34.96%), mean temperature of the coldest quarter (28.30%) and precipitation seasonality (13.58%). The most suitable zone of the temperature seasonality for *K. davidiana* was between 377.4 and 843.4. The highly suitable area was located in the mountainous regions of central and southeast China, which accounted for 13.39% of the whole study area. With climate warming in the future, the highly suitable distribution area of *K. davidiana* was estimated to decrease by 35% (SSP1-2.6 scenario) or 85% (SSP5-8.5 scenario). This study has provided a sufficient scientific basis for the future in situ and ex situ conservation of *K. davidiana*.

Keywords: MaxEnt model; *Keteleeria davidiana*; suitable habitat; climate change

Citation: Zhang, Q.; Shen, X.; Jiang, X.; Fan, T.; Liang, X.; Yan, W. MaxEnt Modeling for Predicting Suitable Habitat for Endangered Tree *Keteleeria davidiana* (Pinaceae) in China. *Forests* **2023**, *14*, 394. https://doi.org/10.3390/f14020394

Academic Editor: Milvia Chicca

Received: 6 January 2023
Revised: 9 February 2023
Accepted: 13 February 2023
Published: 15 February 2023

1. Introduction

A species distribution area reflects the variations in dispersal potential, ecological tolerance and historical evolution among various species [1]. The Sixth Assessment Report (AR6) of the Intergovernmental Panel on Climate Change (IPCC) established that the global surface temperature increased by 1.09 °C in 2011–2020 compared to 1850–1900. By the end of the 21st century, under low greenhouse gas emission scenarios (SSP1-2.6) and high emission scenarios (SSP5-8.5), the global average surface temperature was predicted to increase by 1.3–2.4 °C and 3.3–5.7 °C, respectively, throughout 1850–1900 [2]. The global surface temperature is increasing continuously, accompanied by an increase in annual precipitation [3–5]. The distribution range of ubiquitous species has continued to expand and shrink with climate change, mainly contributed to by temperature and precipitation [6]. Previous research related to the impact of climate change on plants has shown that this anthropogenic climate change might reduce the habitat suitability of plants and even lead to the risk of species becoming endangered [7,8]. Mountainous flora is considered very sensitive to climate change and more vulnerable to the effects of rising temperatures [9].

With declining suitability, the relict plant must evolve to adapt to climate warming [10]. However, the evolution of climate-sensitive arbor is slow due to the long generation time. Rapid climate change will negatively affect the plant population in the original habitat with reduced suitability. In the long process of natural diffusion, the population may have gone extinct before finding a future highly suitable habitat. If plants can spread quickly to the suitable habitats in the future, the risks of plant habitat contraction and population extinction will be greatly decreased. Compared to inefficient natural migration or diffusion, ex situ conservation is a better way to preserve plant population genetic diversity and minimize plant inadaptations to future climates [11–13]. Therefore, predicting the future potential suitable distribution areas under extreme climatic conditions can provide a basis for the ex situ conservation of plants.

Species distribution models (SDMs) are numerical tools used frequently to estimate current geographic distributions of species and to assess the effects of climate change on species distributions [14], as well as habitat suitability [15]. The Maximum Entropy (MaxEnt) model has been widely used in SDMs mainly due to its highly accurate and intuitive predictions [16,17], especially on predicting the impacts of climate change on the potential distribution of relict plants, such as *Thuja sutchuenensis* (Cupressaceae), *Taiwania cryptomerioides* (Cupressaceae) and *Taxus wallichiana* (Taxaceae) [18–20].

Keteleeria davidiana (Bertrand) Beissner (Pinaceae) is a Tertiary relict gymnosperm which prefers a warm and humid subtropical climate [21]. It is also a significant part of the forest vegetation during the transition process of the Yunnan–Guizhou Plateau to the foothills of northwest Guangxi in China [22]. As a tree with mycorrhizal roots, *K. davidiana* has high adaptability and a straight trunk, which is suitable for ornamental purposes. It is a better afforestation pioneer and landscape garden tree species [23]. *K. davidiana* has become an endangered plant due to artificial logging, habitat fragmentation and low reproductive capacity [24–26]. Therefore, it is necessary to carry out scientific conservation and management. The goals of this study were to: (1) identify and quantify the critical climatic variables that influence the distribution of *K. davidiana*; (2) determine the potential geographic distribution of *K. davidiana* in China under current and two future (the 2090s) scenarios and explore the trends of the suitable habitats for *K. davidiana* under the "optimistic" SSP1-2.6 scenario and the "extreme worst" SSP5-8.5 scenario; and (3) propose alternatives for the preservation and sustainable management of the germplasm resources of *K. davidiana*.

2. Materials and Methods

2.1. Information Collation

2.1.1. Occurrence Records of *K. davidiana*

The occurrence records of *K. davidiana* used in this study were obtained from the National Plant Specimen Resource Center (NPSRC; http://www.cvh.ac.cn (accessed on 7 May 2022)) and the Global Biodiversity Information Facility (GBIF; http://www.gbif.org (accessed on 20 May 2022)). A total of 212 occurrence records of *K. davidiana* were obtained between 1939 and 2018 after eliminating duplicate samples (same sampling point and time), ambiguous geographic locations and unnatural specimen data. To reduce the sampling deviation, in each $0.2^{\circ} \times 0.2^{\circ}$ grid, only one record with the closest distance from the center point was selected as the sample distribution record. Finally, 158 valid occurrence records were selected (Figure 1).

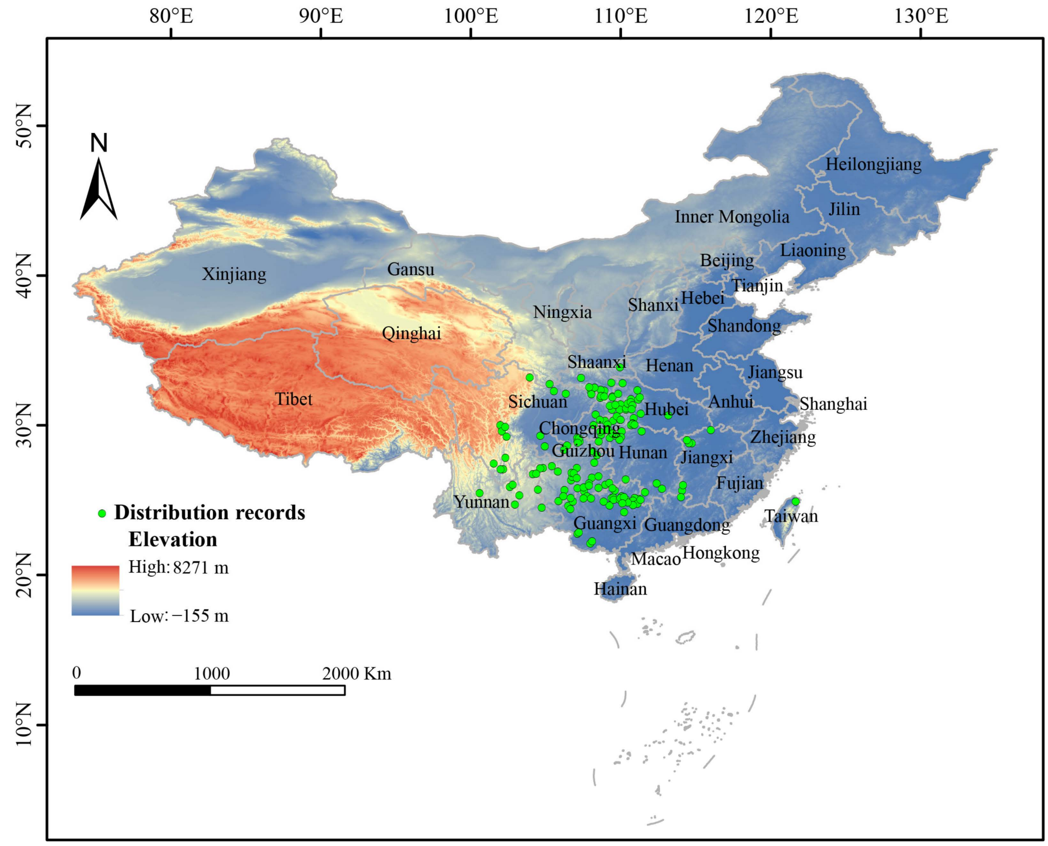

Figure 1. The 158 distribution records of *K. davidiana* in China.

2.1.2. Collection and Selection of Climatic Variables

The bioclimatic variables (Table 1) at 2.5′ spatial resolution for the current (1970–2000) and two future (the 2090s) scenarios were collected from the World Climate Version 2.1 released in 2020 (http://www.worldclim.org/ (accessed on 1 July 2022)). Since the distributions of *K. davidiana* are mainly in the provinces of Hunan, Sichuan, Chongqing, Guizhou, Yunnan, Guangxi and Hubei, at 200–1500 m elevation [27], with little human activity (HA), topography and soil characteristics are not anticipated to change significantly in the coming decades. Assuming that the land was not used in the short term, the BCC-CSM2-MR climate system model was selected as the Global Climate Model (GCM) [28,29]. The climate change scenarios were SSP1-2.6 and SSP5-8.5 for both socio-economic pathways. The low greenhouse gas emission scenario, SSP1-2.6, has a radiation intensity limit of 2.6 W m^{-2} for 2100, while the high greenhouse gas emission scenario, SSP5-8.5, has a radiation intensity limit of 8.5 W m^{-2} for 2100 [2].

In order to avoid the potential correlation between climate variables affecting prediction accuracy, we used R 4.1.1 (https://cran.r-project.org/src/base/R-4/ (accessed on 10 July 2022)) calculations to conduct variance inflation factors (VIFs) and Spearman correlation analysis to screen climatic variables with VIFs less than 10 and correlation coefficients less than 0.8 [30]. A total of six crucial climate variables were kept for predicting the suitable habitat of *K. davidiana* (Table 1).

Table 1. Climatic variables used for modeling the potential suitable habitat of *K. davidiana* in China. The six selected climate variables in modeling are shown in bold.

Variables	Description	Units	Range	Mean ± Std Error
BIO1	Annual mean temperature	°C	2.09–22.08	15.37 ± 0.23
BIO2	Mean diurnal range	°C	5.26–13.12	8.13 ± 0.09
BIO3	Isothermality	/	23.28–49.84	29.62 ± 0.44
BIO4	**Temperature seasonality**	**/**	**443.29–908.53**	**721.61 ± 8.18**
BIO5	Max temperature of warmest month	°C	16.30–33.67	28.81 ± 0.24
BIO6	Min temperature of coldest month	°C	−14.08–10.78	1.07 ± 0.28
BIO7	Temperature annual range	°C	17.85–34.53	27.73 ± 0.21
BIO8	**Mean temperature of wettest quarter**	°C	**9.97–28.16**	**22.20 ± 2.58**
BIO9	Mean temperature of driest quarter	°C	−7.09–16.09	6.50 ± 0.29
BIO10	Mean temperature of warmest quarter	°C	10.60–28.22	23.85 ± 0.24
BIO11	**Mean temperature of coldest quarter**	°C	**−7.09–14.62**	**6.09 ± 0.26**
BIO12	Annual precipitation	mm	716–3198	1281.75 ± 24.66
BIO13	Precipitation of wettest month	mm	118–448	225.62 ± 4.15
BIO14	**Precipitation of driest month**	**mm**	**3–163**	**24.72 ± 1.32**
BIO15	**Precipitation seasonality**	**/**	**35.82–101.07**	**68.06 ± 0.85**
BIO16	Precipitation of wettest quarter	mm	338–1196	605.37 ± 10.93
BIO17	Precipitation of driest quarter	mm	12–522	87.38 ± 4.54
BIO18	**Precipitation of warmest quarter**	**mm**	**330–1044**	**553.36 ± 8.44**
BIO19	Precipitation of coldest quarter	mm	12–522	93.16 ± 5.18

2.2. Modeling Process

2.2.1. Modeling Optimization

The MaxEnt model analyzes and integrates incomplete data to draw inferences or predictions through machine learning and the principle of maximum entropy. Based on the environmental variables and data on species distributions, it simulates species actual and potential distribution areas [31,32]. The MaxEnt was usually run with default parameters when evaluating species distribution. However, this could lead to overfitting and high complexity, which would decrease the accuracy of the study results, thus requiring improved models [33,34]. ENMeval, an R package that can optimize MaxEnt model, regulated two constraint parameters of the model: feature combination (FC) and regularization multiplier (RM). It evaluated the complexity of the model under different parameter combinations and selected a combination of low complexity [35].

The 158 *K. davidiana* occurrence records were divided into four equal parts where possible; three of which were used for training and the remaining part was used for testing [35]. There were a total of 8 RM parameters set: 0.5, 1, 1.5, 2, 2.5, 3, 3.5 and 4 [36]. The MaxEnt model automatically adjusted to the following five characteristics for the FC parameters: linear (L), quadratic (Q), hinge (H), product (P) and threshold (T) [31]. The six feature combinations were L, LQ, H, LQH, LQHP and LQHPT. The ENMeval package was used to test 48 combinations of the above-mentioned parameters. The Akaike information criterion correction (AICc) was used to evaluate the fitting degree and complexity of the model, and the 10% training omission rate (OR10) and the difference between training and testing the area under the curve (AUC.DIFF) were used to assess the extent of the excessive fitting of the model. The combination of parameters as the minimum value of AICc was used as the optimal parameters for constructing the model [35].

2.2.2. Model Simulation

Understanding how well the already available distribution data match future climatic conditions is significant because one crucial reason to consider in modeling is whether the chosen model could reasonably anticipate future habitats using available information. This study imported 158 occurrence records of *K. davidiana* into MaxEnt 3.4.3 [37], along with six bioclimatic variables. The test set was extracted using cross validation. All occurrence records were separated into ten subsets, with one subset serving as the test set and the other nine serving as the training set. The RM parameter was set to 2, the FC parameter was LQHPT, and the maximum number of iterations was 10,000. The data output format was set to logistic and run 10 times repeatedly, and the value of the final output result file was the average of 10 times. MaxEnt generated a raster plot of the distribution probabilities, and the values of each grid cell were expressed in floating point format from 0 to 1 for the occurrence probabilities. The results of the model runs were transformed using ArcGIS 10.8 and classified using the natural discontinuity method to divide suitable habitats into four classes based on gradients: unsuitable habitats (<0.11), lowly suitable habitats (0.11–0.30), moderately suitable habitats (0.30–0.51) and highly suitable habitats (>0.51).

2.2.3. Model Evaluation

The model accuracy was assessed using the receiver operator characteristic curve (ROC) and the area under the ROC curve (AUC). The value of AUC ranged from 0 to 1 [38,39]. The model prediction results were more accurate with the higher value of AUC [40]. An AUC value less than 0.8 indicated low reliability, 0.8–0.9 indicated good accuracy and 0.9–1.0 indicated excellent accuracy [41,42].

2.3. Changes in the Spatial Layout of Suitable Habitats for K. davidiana

A matrix of possible changes in the geographic range of *K. davidiana* under future climate change scenarios was created based on the classification of suitable habitats. We assigned corresponding values to each suitable habitat. Further, according to the matrix, we analyzed the changes in the spatial pattern of the suitable habitat for *K. davidiana* under future SSP1-2.6 and SSP5-8.5 scenarios. Based on the changes in the area of suitable habitats in the present and future, we classified nine types of changes: no change in the area of unsuitable and lowly suitable habitats, no change in the area of moderately suitable habitats, no change in the area of highly suitable habitats, decrease in the area of moderately suitable habitats, drop in the area of highly suitable habitats, the transition from unsuitable and lowly suitable habitats to moderately suitable habitats, the transition from unsuitable and lowly suitable habitats to highly suitable habitats, the transition from highly suitable habitats to moderately suitable habitats and the transition from moderately suitable habitats to highly suitable habitats. ArcGIS 10.8 was used to calculate the number of grids for each suitable habitat and obtain the specific values of the area change [43].

2.4. Assessment of the Importance of Climatic Variables

Using contribution rate (CR), the permutation importance value (PI) and Jackknife, important climatic variables influencing the potential geographic distribution of *K. davidiana* were evaluated. The MaxEnt model recorded the climatic variables with a high contribution rate to the adaptation model in the model during training, improved the gain value of the model by gradually correcting the coefficient corresponding to each eigenvalue and assigned the increased gain value to the dependent value of each eigenvalue, finally expressing the climate contribution as a percentage [19]. The value of the randomly chosen variable at the training point and the ensuing drop in the training AUC value determined the contribution of each climatic variable. The more significant the decline in the AUC value, the more dependent the model was on this climatic variable [44]. After a Jackknife test on a single climate variable, when all-important climatic variables were combined to produce results, the training gain values, test gain values, and AUC values were compared to assess the importance of climatic variables [19].

2.5. Analysis of Multiple Environmental Similarity Surface (MESS) and the Most Dissimilar (MoD)

The magnitude of current and future climate anomalies was evaluated using MESS, and the key factors influencing likely changes in regional distribution were analyzed using MoD. MESS measured how similar the climatic conditions of a certain point in a given period were to the reference layer (S). When S > 0, the smaller the value of S, the more significant the difference between the climatic variables at that point and the reference layer was. S = 100 indicated that there was no difference between the reference layer and the climatic variables; S $\leq$ 0 showed that at least one climatic variable value was outside of the reference point's climate range, and the larger the negative value, the greater the degree of climate anomaly [45]. The most dissimilar (MoD) was the climatic variable with the lowest S value for a given position on the reference layer. MoD denoted the variable with the highest degree of abnormality and might be the primary cause of the shift in geographic distribution [45].

3. Results

3.1. Optimization and Accuracy Evaluation of the Model

The model had the minimum AlCc value when RM = 2 and FC = LQHPT, i.e., AICc = 0, using the ENMeval program to optimize the parameter of the MaxEnt model (Figure 2). This parameter setting significantly decreased the complexity of the model and enhanced the fitness, as indicated by the fact that AUC.DIFF and OR10 were 13.72% and 42.86% less than the default values (RM = 1 and FC = LQHPT). As a result, in this study, RM = 2 and FC = LQHPT were selected as ideal model parameters. According to the receiver operator characteristic curves (ROCs), the model mean training AUC was 0.8771 (with a standard error of 0.0016), and its mean test AUC was 0.8479 (with a standard error of 0.0105), suggesting the accuracy of the prediction.

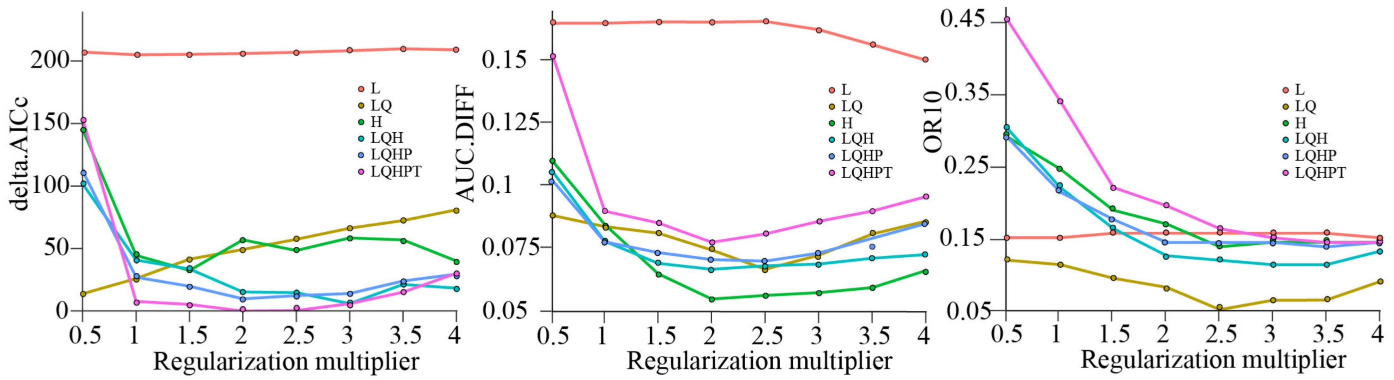

Figure 2. OR10, AUC.DIFF and delta.AICc for *K. davidiana* from MaxEnt model under different parameter combinations.

3.2. Assessment of Crucial Climatic Variables

Table 2 displays the crucial elements of six climatic variables in determining the potential suitability of the current habitat for *K. davidiana*. Temperature seasonality (BIO4), the mean temperature of the coldest quarter (BIO11) and precipitation seasonality (BIO15) were the three variables with the highest contribution rate (CR), with a combined contribution rate of 76.84%. The BIO4, BIO11 and the mean temperature of the wettest quarter (BIO8) were the three variables with the highest permutation importance (PI), with a cumulative value of 87.36%. Three variables with the highest regularized training gain and test gain during the univariate simulation period were BIO4, BIO11 and the precipitation of the warmest quarter (BIO18), and the three highest AUC values were those of BIO4, BIO15 and BIO18. These climatic variables showed a good fit to the model and contained more valid information. The BIO4, BIO8 and BIO15 had the most significant decreases in the regularized training gain, test gain and AUC values when simulated for a non-specific variable, indicating that these variables contained information that was not present in the other variables. According to the above analysis, BIO4, BIO8 and BIO11 were the main temperature factors which affect the current geographical distribution of *K. davidiana*, while BIO18 was the main precipitation factor.

Table 2. The contribution rate and value of gain of climatic variables.

Variables	CR (%)	PI (%)	RTG_W	RTG_O	TG_W	TG_O	AUC_W	AUC_O
BIO4	34.96	31.72	0.6870	0.4129	0.7536	0.4669	0.8248	0.7636
BIO8	7.63	18.87	0.7780	0.2362	0.7984	0.2955	0.8370	0.7184
BIO11	28.30	36.77	0.7735	0.3437	0.8514	0.3660	0.8415	0.7088
BIO14	2.67	4.32	0.8193	0.2120	0.8688	0.2481	0.8460	0.7045
BIO15	13.58	3.99	0.7872	0.3008	0.8343	0.3264	0.8411	0.7257
BIO18	12.87	4.33	0.8275	0.3205	0.8965	0.3521	0.8517	0.7242

CR: contribution rate, PI: permutation importance value; RTGw: regularization training gain without this variable; RTG_O: regularization training gain only with this variable; TG_W: test gain without this variable; TG_O: test gain only with variable; AUC_W: AUC without this variable; AUC_O: AUC only with this variable.

3.3. Response Curve Analysis of Important Climatic Variables

A response curve from the logistic regression analysis of the MaxEnt model illustrated the relationship between the probability of *K. davidiana* occurrence and climatic parameters. It explained how each climatic condition influenced the distribution of suitable habitats. When the occurrence possibility was above 0.5, the growth in related climate elements was beneficial to the growth in plants. The four most significant climatic variables that affected the existing range of potential suitable habitats for *K. davidiana* are shown as response curves in Figure 3.

When BIO4 increased within a specific range, the likelihood of *K. davidiana* increased (34.96% contribution and 31.72% replacement importance) (Figure 3A). The chance was more significant than 0.5 when the variance fell within the 377.4–843.4 range. As a result, the range of BIO4 was suitable for the growth of *K. davidiana*. Similar results were obtained for BIO8 with a suitable degree of 10.32–31.3 °C (Figure 3B), BIO11 with an appropriate degree of −9.05–11.5 °C (Figure 3C) and BIO18 with a suitable range of 265.8–2295.4 mm (contribution rate of 12.87%; permutation importance of 4.33%).

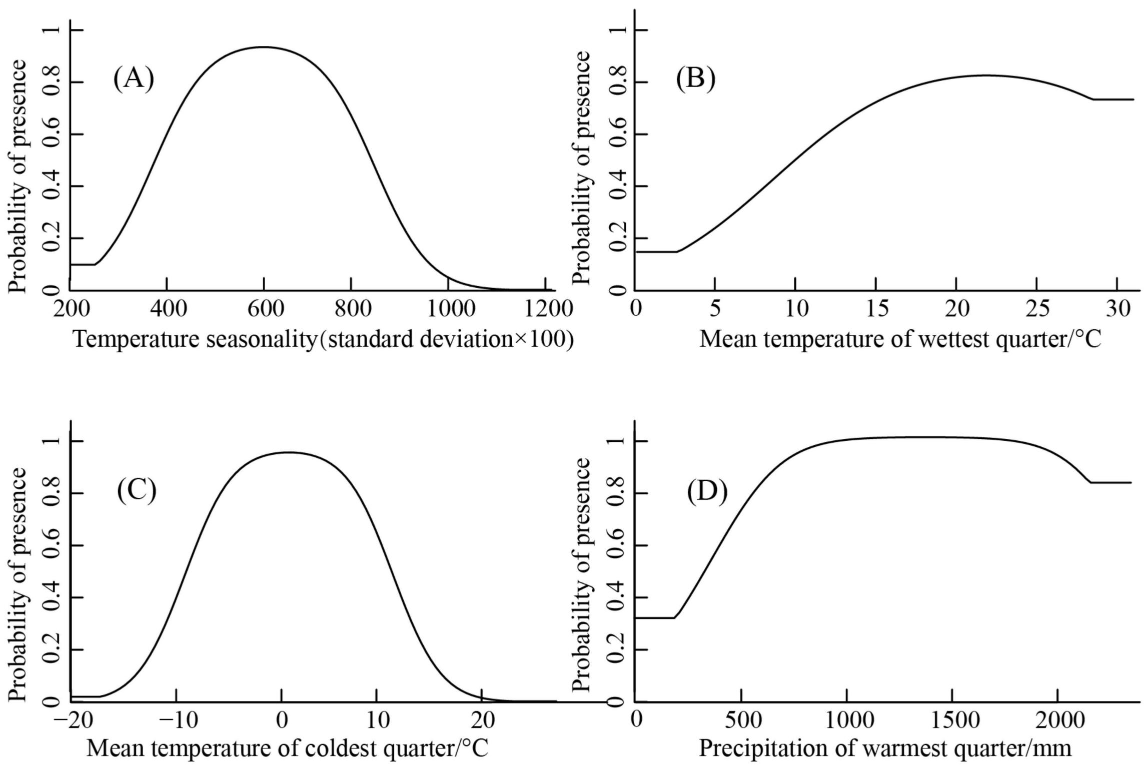

Figure 3. Response curves of important climatic variables. (**A**) Temperature seasonality (BIO4); (**B**) Mean temperature of wettest quarter (BIO8); (**C**) Mean temperature of coldest quarter (BIO11) and (**D**) Precipitation of warmest quarter (BIO18).

3.4. Potential Suitable Habitat for K. davidiana under Current Climatic Conditions

The proportions of 158 occurrence records of *K. davidiana* in different suitable habitats are in the order of highly suitable habitat (67.72%), moderately suitable habitat (16.46%), lowly suitable habitat (11.39%) and unsuitable habitat (4.43%), indicating that the potential suitable habitats simulated by the optimized MaxEnt could basically cover these occurrence records.

The existing potential suitable habitat distribution of *K. davidiana* in China appears in Figure 4. The suitable habitat is 2.4 million km^2, accounting for 51% of the study area. Most of the highly suitable habitats are located in the southern Qinling Mountains, Daba Mountains, Wushan Mountains, Wudang Mountains, Wuling Mountains, Yunnan–Guizhou Plateau, Nanling Mountains, Wuyi Mountains and other mountainous areas, covering 63.14 $\times$ 10^4 km^2, which accounts for 13.39% of the study area. The moderately suitable habitat includes Sichuan Basin, Wumeng Mountains, eastern Nanling and lower elevation areas around the Wuyi Mountains, with an area of 69.87 $\times$ 10^4 km^2, accounting for 14.82% of the whole study area. The lowly suitable habitat is mainly concentrated in the Hengduan Mountains, the western part of the Yunnan–Guizhou Plateau, the hills of Guangdong and Guangxi, the mountains of Jiangnan and the hills of Zhejiang and Fujian, with an area of 107.13 $\times$ 10^4 km^2, accounting for 22.72% of the entire study area.

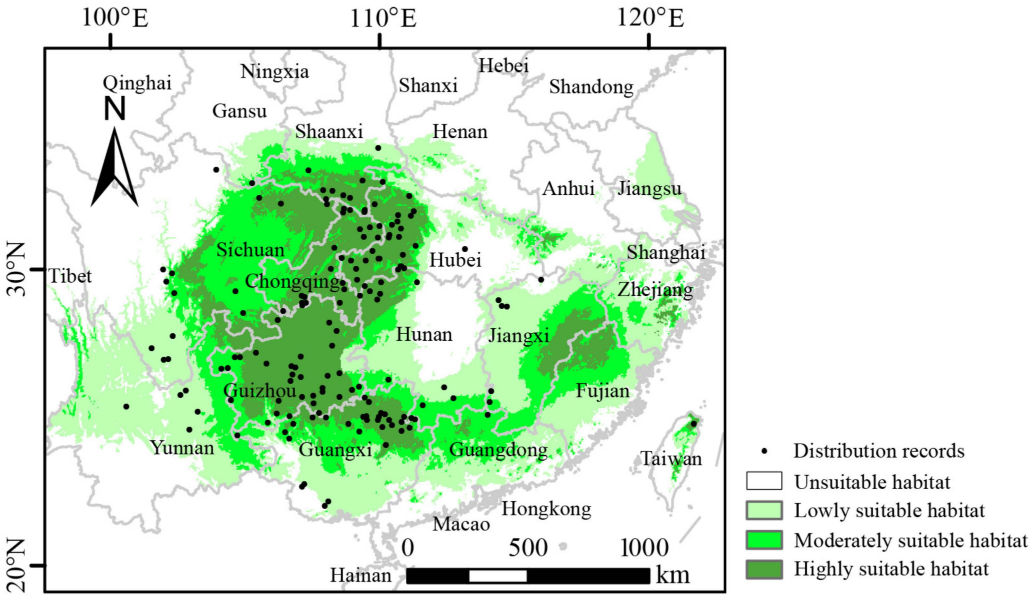

Figure 4. Potential suitable habitat for *K. davidiana* under current climatic conditions.

3.5. Dynamics of Potential Suitable Habitats for K. davidiana under Different Future Climate Scenarios

The potential suitable habitat for *K. davidiana* is shown in Figure 5 under the climate change scenarios SSP1-2.6 and SSP5-8.5 in the 2090s. Under the SSP1-2.6 climatic scenario (Figure 5A), the highly suitable habitat, moderately suitable habitat, lowly suitable habitat and unsuitable habitat, respectively, account for 8.71%, 12.22%, 27.43% and 51.64% of the whole study area, while the ratio is 2.06%, 10.63%, 25.25% and 62.06% under the SSP5-8.5 climate scenario (Figure 5B).

The highly and moderately suitable habitats for *K. davidiana* will shrink in different degrees, according to a comparison between the current suitable habitat and the predicted suitable habitat under the two future scenarios (Figure 6). Under the SSP1-2.6 and SSP5-8.5 scenarios, the highly suitable habitat will reduce by 22.1 $\times$ 10^4 km^2 and 53.4 $\times$ 10^4 km^2, and the moderately suitable habitat will reduce by 12.4 $\times$ 10^4 km^2 and 19.9 $\times$ 10^4 km^2, while the lowly suitable habitat will increase by 22.21 $\times$ 10^4 km^2 and 11.93 $\times$ 10^4 km^2, respectively.

Compared with the current suitable habitats, the changes in suitable habitats in the future will mainly show a decrease in the suitability of *K. davidiana* in the Sichuan Basin, Nanling, Wuyi Mountains and so on. In contrast, the suitability of *K. davidiana* in the Xuefeng Mountains, Qinling Mountains and Hengduan Mountains will increase. The results indicate that the suitable habitats for *K. davidiana* show a migration trend to higher elevations.

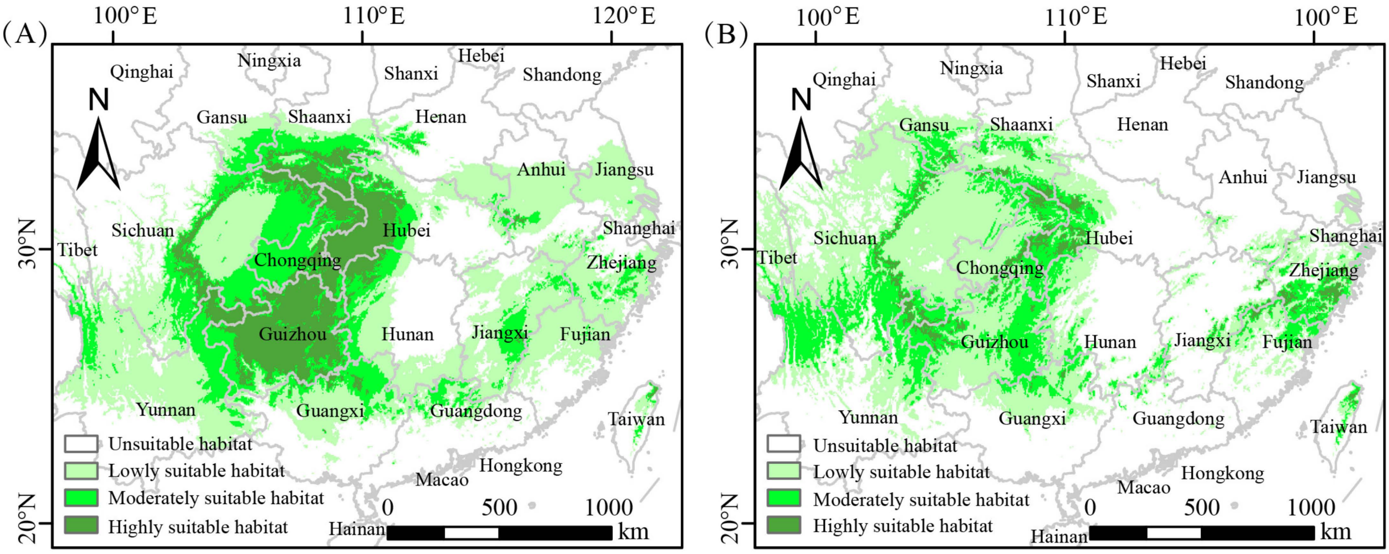

Figure 5. Potential suitable habitat for *K. davidiana* under SSP1-2.6 (**A**) and SSP5-8.5 (**B**) climatic conditions in the 2090s.

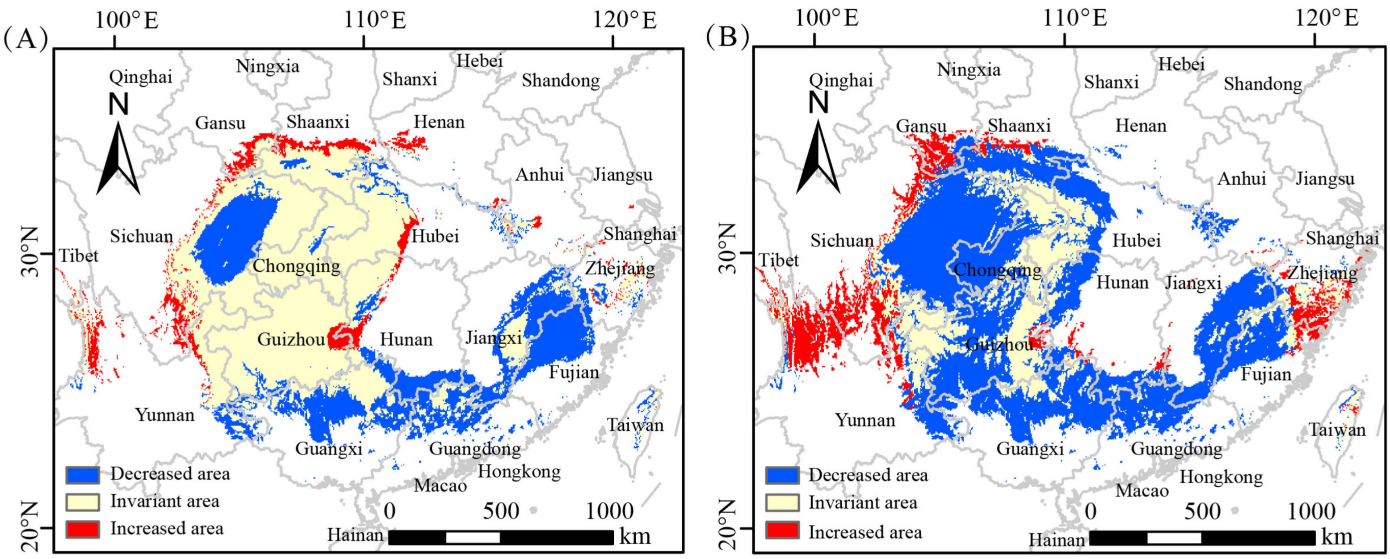

Figure 6. Change in the highly and moderately potential suitable habitats for *K. davidiana* under SSP1-2.6 (**A**) and SSP5-8.5 (**B**) climatic conditions in the 2090s.

3.6. Analysis of MESS and MoD Variables

Figure 7 displays the multivariate environmental similarity surface (MESS) and most dissimilar variable (MoD) for the two 2090s climate scenarios and the current environment. The SSP5-8.5 climate scenario has low multiple similarities and a high degree of climate anomalies, because the average similarity is −6.44 and 1.18 in the SSP5-8.5 and SSP1-2.6 scenarios, and the percentage of negative similarity is 59.279% and 0.008%, respectively. The suitable habitats in central and southern China are the main climate anomaly areas ($S \leq 0$) in the SSP1-2.6 scenario, in which the MoD is BIO4, BIO8 and BIO11. Under the SSP5-8.5

scenario, the prominent climate anomalies appear in the suitable habitats in low-elevation areas, and the MoD is BIO4, BIO8 and BIO11.

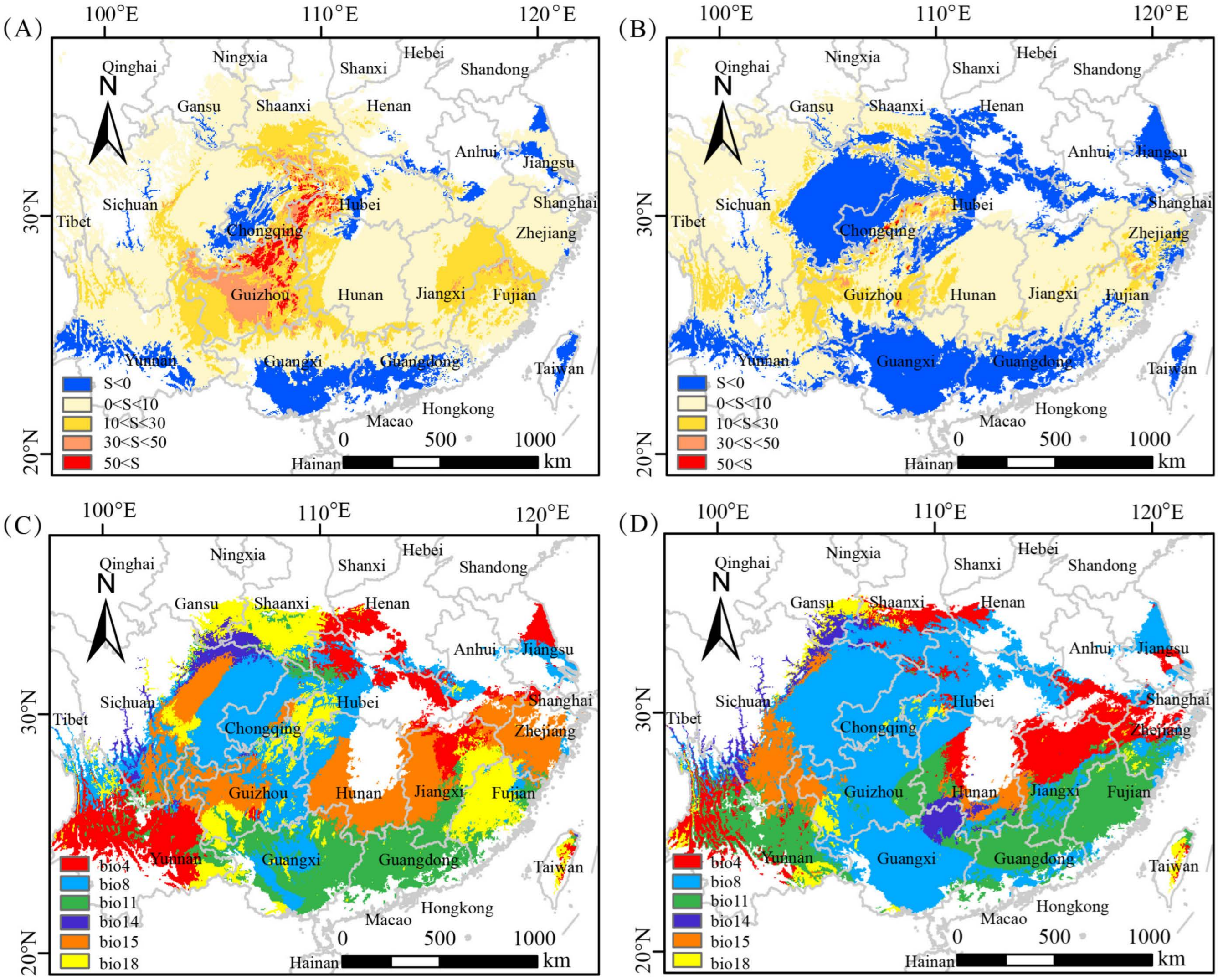

Figure 7. MESS and MoD for *K. davidiana* under climatic conditions in the 2090s. (**A**) MESS for SSP1-2.6 scenario; (**B**) MESS for SSP5-8.5 scenario; (**C**) MoD for SSP1-2.6 scenario and (**D**) MoD for SSP5-8.5 scenario.

3.7. Analysis between the Highly Suitable Habitat Areas and NPAs

Figure 8 displays the highly suitable habitat areas of *K. davidiana* under current climates and the natural protected areas (NPAs) in China. *K. davidiana* in the current highly suitable habitat and NPAs, respectively, account for 67.72% and 18.35% of the total 158 occurrence records. There are 20 distribution records overlapping the limits of NPAs with the current highly suitable habitat, which account for 12.66% of the total 158 occurrence records.

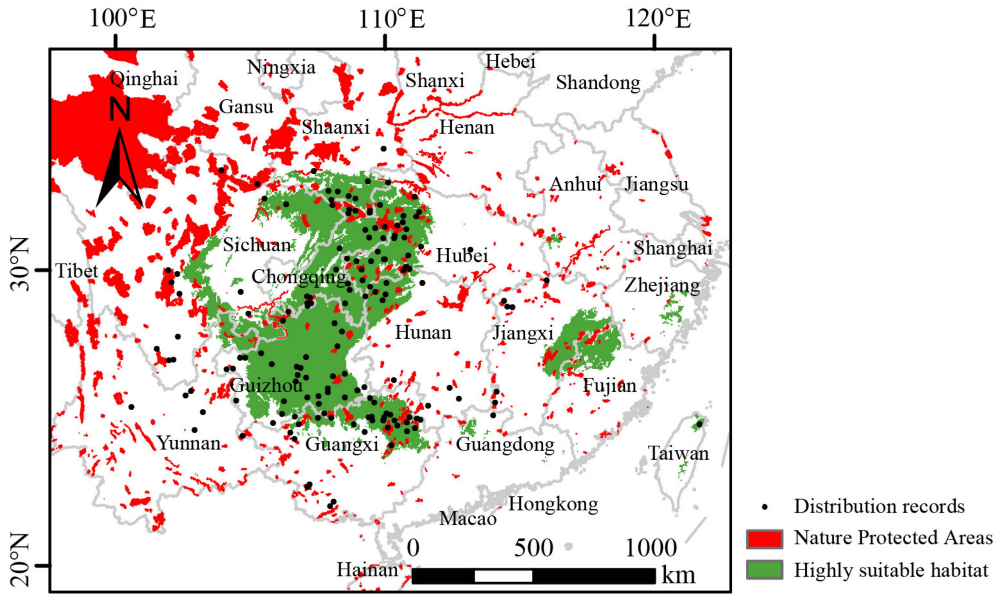

Figure 8. The highly suitable habitat for *K. davidiana* under current climates and NPAs.

4. Discussion

4.1. Ecology of K. davidiana

Under current climatic conditions, the distribution areas of *K. davidiana* were mainly in the Daba–Wushan Mountains, the Yunnan–Guizhou Plateau and other mountainous regions at an altitude of 200–1500 m in China [27]. *Keteleeria davidiana* is often mixed with conifer and broad-leaved trees such as *Pinus massoniana* (Pinaceae), *Cunninghamia lanceolata* (Cupressaceae) and *Quercus variabilis* (Fagaceae). *Keteleeria davidiana* is also sporadically found in the Qinling Mountains, the Wuling Mountains and the Nanling Mountains. These areas had moderate temperatures and sufficient rainfall in summer and belonged to the subtropical forests of warm coniferous forests.

Keteleeria davidiana has a wide distribution range, which is the most cold-resistant species of *Keteleeria*. However, its distribution area occupancy is not high, which is not only affected by HA, but is also affected by ecological factors such as temperature and precipitation. Different combinations of temperature and precipitation may affect trees differently [46]. Additionally, other trees react to climate change differently [47]. As a result, *K. davidiana* might be suited to a particular climate, commonly known as "matching species with the site" in China. According to the assessment of critical climatic variables, the distributions of *K. davidiana* were strongly influenced by the seasonal effects of temperature, average temperature and precipitation in summer and the average temperature in winter.

4.2. Analysis of the Current Potential Suitable Habitat for K. davidiana

The Daba Mountains, Wushan Mountains and Yungui Plateau are also the main distribution areas of *K. davidiana*. The Wuyi Mountains in eastern China were a highly suitable area with no distribution of *K. davidiana*, which may be due to the impact of distance isolation and not enough time for the species to spread. The moderately suitable habitat of *K. davidiana* was mainly located in the Sichuan Basin and Nanling, where the temperature was high in summer and dry in winter [48,49]. Its distribution in this area was scarce. The lowly suitable habitat of *K. davidiana* was mainly distributed in the Hengduan Mountains with complex topography conditions, pronounced dry and wet seasons and significant climatic differences, and in the hills of Guangdong and Guangxi, and the mountains of Jiangnan, where summer is hot and long-lasting, and winter is cold and dry. *Keteleeria davidiana* was susceptible to growth inhibition and little distribution. In a way, due to climate restriction, the growth of *K. davidiana* has noticeable zonal differences. The climatic characteristics of the highly suitable habitat were abundant rain and moderate temperature (Figure 4).

The spatial occupancy of species distribution is also closely related to human activity (HA). HA can reduce the distribution ranges of endangered species but expand those of eurycholic species [50]. For example, Chinese fir (*Cunninghamia lanceolata*) is one of the fast-growing timber species and is widely cultivated in subtropical southern China [38], and the spatial occupancy of Chinese fir has been expanded to the high suitability area of *K. davidiana*. Due to the negative impacts of human activities, *K. davidiana* has a lower range in the high suitability area. Now, the Chinese government hopes to achieve carbon neutrality through afforestation. In the future, *K. davidiana* with a long survival period can become one of the suitable main tree species for carbon sink forests.

4.3. Changes in the Suitable Habitat for K. davidiana

Different suitable habitats were affected by various climate elements in the two future climate scenarios of the "optimistic" SSP1-2.6 scenario and the "extreme worst" SSP5-8.5 scenario, leading to varying degrees of growth and decreases in habitat suitability. Climate warming has caused the immigration of warm conifers at high altitudes to cold-adapted plant distribution areas [51]. However, there were various reasons for the increase in the suitability of *K. davidiana* in different high-altitude regions. Due to the increase in precipitation, the southern side of the Qinling Mountains was no longer subject to the local precipitation constraints. Nevertheless, the suitable region was only expanded slightly due to the Qinling Mountains' steepness (http://www.bigemap.com/reader/hcontour/ (accessed on 15 August 2022)). On account of warming and the lifting of temperature restrictions, high mountain areas such as the Hengduan Mountains and the Xuefeng Mountains improved in suitability, changing from low suitability to medium suitability habitats [52]. In addition, because the SSP5-8.5 scenario increased the temperature in the area more than the SSP1-2.6 scenario, the SSP5-8.5 scenario was more suitable for the Hengduan Mountains than the SSP1-2.6 scenario. Overall, compared to the SSP1-2.6 scenario, the SSP5-8.5 scenario boosted suitability over a broader area.

Although climate warming could increase the suitability of *K. davidiana* in some areas to varying degrees, there was a greater degree of suitability decline in other locations, and the reasons for the decrease in suitability in different regions were also various. For instance, the Sichuan Basin's habitat suitability decreased from moderate to low, most likely due to an increase in average summer temperature that hampered the growth of *K. davidiana*. Under the SSP1-2.6 scenario, the highly suitable habitats of the Yunnan–Guizhou Plateau dropped to moderately suitable habitats, and the moderately suitable habitats of the Nanling Mountains dropped to lowly suitable habitats. However, under the SSP5-8.5 scenario, the highly suitable habitat areas of the Yunnan–Guizhou Plateau dropped to lowly suitable habitats, while the moderately suitable habitats of the Nanling disappeared directly. Under the changes in temperature and precipitation of the optimistic SSP1-2.6 scenario, places such as the Wuyi Mountains and their vicinity changed from highly suitable areas to lowly suitable habitats. Nevertheless, most of the regions dropped to unsuitable habitats under the SSP5-8.5 scenario. The potential suitability of *K. davidiana* would decline, and fragmentation would rise regardless of the future climate scenarios. The suitable habitat area decreased more in the SSP5-8.5 scenario than in the SSP1-2.6 scenario.

4.4. Suggestions for Conservation Strategies and Assisted Migration

Although there are 67.72% distribution records in the highly suitable habitat of *K. davidiana* (Figure 4), only 18.35% is in the NPAs, and 12.66% is overlapping the NPAs with the current highly suitable habitat (Figure 8). The highly suitable habitat of *K. davidiana* will be significantly reduced by 35% and 85%, respectively, in the "optimistic" SSP1-2.6 scenario and the "extreme worst" SSP5-8.5 scenario (Figure 5). Therefore, it is urgent and necessary to make conservation strategies.

Among the current distribution areas of *K. davidiana*, the highly suitable areas predicted under the "optimistic" SSP1-2.6 scenario and the "extreme worst" SSP5-8.5 scenario could be used as in situ conservation areas, and the promotion of the conservation of these areas also contributes to maintaining ecosystem stability. The NPAs in the highly suitable areas without *K. davidiana* distribution should be the first migration protection areas.

In the Yunnan–Guizhou Plateau, the suitability of highly suitable areas will decrease, which could result in a decline in the population richness of the currently dispersed *K. davidiana* and the risk of loss of rare alleles. Although there are only scarce distributions of *K. davidiana* in the Nanling Mountains, there is a risk of a loss of genetic diversity when it decreases from a moderately suitable habitat to a lowly suitable habitat. Therefore, it is recommended to protect *K. davidiana* in the Yunnan–Guizhou Plateau and Nanling via ex situ conservation, and transplant the plants to highly suitable habitats without *K. davidiana* under future climate scenarios to reduce the risk of a loss of genetic diversity.

Due to the lower distribution of *K. davidiana* in the Sichuan Basin and Wuyi Mountains, the reduction in the suitability will not have a tremendous adverse effect on the survival of *K. davidiana*. It will just narrow the potential expansion of *K. davidiana* under future climate scenarios. In the future climate scenario, the south of the Qinling Mountains and Hengduan Mountains, and the east of the Wuyi Mountains, are newly increased highly and moderately suitable areas, but they will not lead to the natural spread of *K. davidiana* due to the fragmentation of the habitats in these areas. It is best to use transplanted plants in these areas.

5. Conclusions

In this study, the optimized MaxEnt model was used to predict the potential suitable habitat of *K. davidiana* in China under optimistic and extreme worst climate change scenarios. Temperature and precipitation are important factors affecting the suitability of the *K. davidiana* habitat, and temperature plays a more prominent role than precipitation. Under different climate change scenarios in the future, the suitability of potential habitats of *K. davidiana* will decrease, especially under extreme worst climate change scenarios, and the suitable habitat area will decrease more. In addition, some suitable habitats of *K. davidiana* may migrate to high altitudes in the 2090s. At present and in the future, it is recommended to use the highly suitable habitats for the in situ conservation of *K. davidiana*; in particular, the NPAs in the highly suitable areas can be the first migration protection areas. The increased highly and moderately suitable habitats in the future can be cultivated with conservation purposes. This study provided a theoretical reference for the biological conservation and sustainable scientific management of *K. davidiana*.

Author Contributions: Q.Z.: conceptualization, methodology, formal analysis, data curation, writing—original draft and writing—review and editing. X.S.: conceptualization, methodology, software, visualization and writing—review and editing. X.J. and T.F.: writing—review and editing. X.L. and W.Y.: methodology, resources, writing—review and editing, validation, supervision and funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by "National Key R & D Program of China, grant number 2020YFA0608100", "Special funding for innovative construction in Hunan province, grant number 2021ZK4226", "the Scientific Research Foundation of Hunan Provincial Education Department, grant number 18B171" and the program of National Key (cultivating) Disciplines in Central South University of Forestry and Technology.

Data Availability Statement: Not applicable.

Acknowledgments: We gratefully acknowledge the kind support of the National Engineering Laboratory for Applied Technology of Forestry and Ecology in South China, and Key Laboratory of Urban Forest Ecology of Hunan Province.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Li, L.P.; He, S.Y.; Jiang, Y.M.; Wang, T.; Zhao, H.H.; Cui, W.H.; Zhang, Y.M.; Hai, Y.; Wan, H.W. Species range size patterns and their significance on biodiversity conservation. *Sci. Sin. Vitae* **2019**, *49*, 929–937. [CrossRef]
2. Pörtner, H.O.; Roberts, D.C.; Tignor, M.; Poloczanska, E.S.; Mintenbeck, K.; Alegría, A.; Craig, M.; Langsdorf, S.; Löschke, S.; Möller, V.; et al. Summary for Policymakers. In *Climate Change 2022: Impacts, Adaptation and Vulnerability*; Intergovernmental Panel on Climate Change: Cambridge, UK; New York, NY, USA, 2022; pp. 1–24.
3. Thackeray, C.W.; Hall, A.; Norris, J.; Chen, D. Constraining the increased frequency of global precipitation extremes under warming. *Nat. Clim. Chang.* **2022**, *12*, 441–448. [CrossRef]
4. Bellard, C.; Bertelsmeier, C.; Leadley, P.; Thuiller, W.; Courchamp, F. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **2012**, *15*, 365–377. [CrossRef] [PubMed]
5. Jia, X.; Ma, F.F.; Zhou, W.M.; Zhou, L.; Yu, D.P.; Qin, J.; Dai, L.M. Impacts of climate change on the potential geographical distribution of broadleaved Korean pine (*Pinus koraiensis*) forests. *Acta Ecol. Sin.* **2017**, *37*, 464–473. [CrossRef]
6. Zhao, G.; Cui, X.; Sun, J.; Li, T.; Wang, Q.; Ye, X.; Fan, B. Analysis of the distribution pattern of Chinese *Ziziphus jujuba* under climate change based on optimized biomod2 and MaxEnt models. *Ecol. Indic.* **2021**, *132*, 108256. [CrossRef]
7. Cai, C.; Zhang, X.; Zha, J.; Li, J.; Li, J. Predicting Climate Change Impacts on the Rare and Endangered *Horsfieldia tetratepala* in China. *Forests* **2022**, *13*, 1051. [CrossRef]
8. Liu, M.-L.; Sun, H.-Y.; Jiang, X.; Zhou, T.; Zhang, Q.-J.; Su, Z.-D.; Zhang, Y.-N.; Liu, J.-N.; Li, Z.-H. Simulation and Prediction of the Potential Geographical Distribution of *Acer cordatum* Pax in Different Climate Scenarios. *Forests* **2022**, *13*, 1380. [CrossRef]
9. Telwala, Y.; Brook, B.W.; Manish, K.; Pandit, M.K. Climate-Induced Elevational Range Shifts and Increase in Plant Species Richness in a Himalayan Biodiversity Epicentre. *PLoS ONE* **2013**, *8*, e57103. [CrossRef]
10. Gougherty, A.V.; Keller, S.R.; Fitzpatrick, M.C. Maladaptation, migration and extirpation fuel climate change risk in a forest tree species. *Nat. Clim. Chang.* **2021**, *11*, 166–171. [CrossRef]
11. Vitt, P.; Havens, K.; Kramer, A.T.; Sollenberger, D.; Yates, E.D. Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biol. Conserv.* **2010**, *143*, 18–27. [CrossRef]
12. Williams, M.I.; Dumroese, R.K. Preparing for Climate Change: Forestry and Assisted Migration. *J. For.* **2013**, *111*, 287–297. [CrossRef]
13. Aitken, S.N.; Whitlock, M.C. Assisted Gene Flow to Facilitate Local Adaptation to Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **2013**, *44*, 367–388. [CrossRef]
14. Jiménez-García, D.; Peterson, A.T. Climate change impact on endangered cloud forest tree species in Mexico. *Rev. Mex. Biodivers.* **2019**, *90*, 1–14. [CrossRef]
15. Elith, J.; Leathwick, J.R. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu. Rev. Ecol. Evol. Syst.* **2009**, *40*, 677–697. [CrossRef]
16. Khan, A.M.; Li, Q.T.; Saqib, Z.; Khan, N.; Habib, T.; Khalid, N.; Majeed, M.; Tariq, A. MaxEnt Modelling and Impact of Climate Change on Habitat Suitability Variations of Economically Important Chilgoza Pine (*Pinus gerardiana* Wall.) in South Asia. *Forests* **2022**, *13*, 715. [CrossRef]
17. Rong, Z.; Zhao, C.; Liu, J.; Gao, Y.; Zang, F.; Guo, Z.; Mao, Y.; Wang, L. Modeling the Effect of Climate Change on the Potential Distribution of Qinghai Spruce (*Picea crassifolia* Kom.) in Qilian Mountains. *Forests* **2019**, *10*, 62. [CrossRef]
18. Qin, A.; Liu, B.; Guo, Q.; Bussmann, R.W.; Ma, F.; Jian, Z.; Xu, G.; Pei, S. Maxent modeling for predicting impacts of climate change on the potential distribution of *Thuja sutchuenensis* Franch., an extremely endangered conifer from southwestern China. *Glob. Ecol. Conserv.* **2017**, *10*, 139–146. [CrossRef]
19. Zhao, H.; Zhang, H.; Xu, C. Study on *Taiwania cryptomerioides* under climate change: MaxEnt modeling for predicting the potential geographical distribution. *Glob. Ecol. Conserv.* **2020**, *24*, e01313. [CrossRef]
20. Wu, X.; Wang, M.; Li, X.; Yan, Y.; Dai, M.; Xie, W.; Zhou, X.; Zhang, D.; Wen, Y. Response of distribution patterns of two closely related species in *Taxus* genus to climate change since last inter-glacial. *Ecol. Evol.* **2022**, *12*, e9302. [CrossRef]
21. Wang, C.Y.; Ma, S.B.; Dang, C.L. Ecological and geographical distribution of *Keteleeria* and its systematic evolution in China. *Guihaia* **2012**, *32*, 612–616. [CrossRef]
22. Lu, Y.X.; Liang, C.F. General information and fundamental features of plant geography of Guangxi. *Guihaia* **1983**, *3*, 153–165.
23. Qiu, X.J.; Wang, H.Z. *Ecological Garden Tree Species in Southern China*; Guangxi Science and Technology Press: Guangxi, China, 2006; pp. 211–212.
24. Mou, F.J.; Dai, X.F.; Li, S.Z.; Xu, Q.H. The Advance of Studies on *Keteleeria*. *J. West China Forest Sci.* **2012**, *6*, 92–99. [CrossRef]
25. Wang, S.; Xie, Y. *China Species Red List-Plants*; Higher Education Press: Beijing, China, 2004; p. 48.
26. Ma, Y.; Chen, G.; Grumbine, R.E.; Dao, Z.; Sun, W.; Guo, H. Conserving plant species with extremely small populations (PSESP) in China. *Biodivers. Conserv.* **2013**, *22*, 803–809. [CrossRef]
27. Fu, L.; Li, N.; Mill, R.R. Pinaceae. In *Flora of China*; Wu, Z., Raven, P.H., Hong, D., Eds.; Science Press: Beijing, China; Missouri Botanical Press: St. Louis, MO, USA, 1999; Volume 4, pp. 11–52. Available online: http://www.iplant.cn/foc/pdf/Pinaceae.pdf. (accessed on 19 June 2022).
28. Popp, A.; Calvin, K.; Fujimori, S.; Havlik, P.; Humpenöder, F.; Stehfest, E.; Bodirsky, B.L.; Dietrich, J.P.; Doelmann, J.C.; Gusti, M.; et al. Land-use futures in the shared socio-economic pathways. *Glob. Environ. Chang.* **2017**, *42*, 331–345. [CrossRef]

29. Wu, T.; Lu, Y.; Fang, Y.; Xin, X.; Li, L.; Li, W.; Jie, W.; Zhang, J.; Liu, Y.; Zhang, L.; et al. The Beijing Climate Center Climate System Model (BCC-CSM): The main progress from CMIP5 to CMIP6. *Geosci. Model Dev.* **2019**, *12*, 1573–1600. [CrossRef]
30. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; Marquéz, J.R.G.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **2013**, *36*, 27–46. [CrossRef]
31. Phillips, S.J.; Anderson, R.P.; Schapire, R.E. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **2006**, *190*, 231–259. [CrossRef]
32. Jiménez-Valverde, A.; Peterson, A.T.; Soberón, J.; Overtonet, J.M.; Aragón, P.; Lobo, J.M. Use of niche models in invasive species risk assessments. *Biol. Invasions* **2011**, *13*, 2785–2797. [CrossRef]
33. Warren, D.L.; Wright, A.N.; Seifert, S.N.; Shaffer, H.B. Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. *Divers. Distrib.* **2013**, *20*, 334–343. [CrossRef]
34. Warren, D.L.; Seifert, S.N. Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* **2011**, *21*, 335–342. [CrossRef]
35. Muscarella, R.; Galante, P.J.; Soley-Guardia, M.; Boria, R.A.; Kass, J.M.; Uriarte, M.; Anderson, R.P. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxentecological niche models. *Methods Ecol. Evol.* **2015**, *5*, 1198–1205. [CrossRef]
36. Elith, J.; Phillips, S.J.; Hastie, T.; Dudík, M.; Chee, Y.E.; Yates, C.J. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **2011**, *17*, 43–57. [CrossRef]
37. Phillips, S.J.; Anderson, R.P.; Dudík, M.; Schapire, R.E.; Blair, M.E. Opening the black box: An open-source release of Maxent. *Ecography* **2017**, *40*, 887–893. [CrossRef]
38. Zhao, Y.; Deng, X.; Xiang, W.; Chen, L.; Ouyang, S. Predicting potential suitable habitats of Chinese fir under current and future climatic scenarios based on Maxent model. *Ecol. Informatics* **2021**, *64*, 101393. [CrossRef]
39. Zhang, K.; Liu, Z.; Abdukeyum, N.; Ling, Y. Potential Geographical Distribution of Medicinal Plant *Ephedra sinica* Stapf under Climate Change. *Forests* **2022**, *13*, 2149. [CrossRef]
40. Fielding, A.H.; Bell, J.F. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **1997**, *24*, 38–49. [CrossRef]
41. Kurpis, J.; Serrato-Cruz, M.A.; Arroyo, T.P.F. Modeling the effects of climate change on the distribution of *Tagetes lucida* Cav. (Asteraceae). *Glob. Ecol. Conserv.* **2019**, *20*, e00747. [CrossRef]
42. Alfonso-Corrado, C.; Naranjo-Luna, F.; Clark-Tapia, R.; Campos, J.E.; Rojas-Soto, O.R.; Luna-Krauletz, M.D.; Bodenhorn, B.; Gorgonio-Ramírez, M.; Pacheco-Cruz, N. Effects of Environmental Changes on the Occurrence of *Oreomunnea mexicana* (Juglandaceae) in a Biodiversity Hotspot Cloud Forest. *Forests* **2017**, *8*, 261. [CrossRef]
43. Ye, X.; Zhao, G.-H.; Zhang, M.-Z.; Cui, X.-Y.; Fan, H.-H.; Liu, B. Distribution Pattern of Endangered Plant *Semiliquidambar cathayensis* (Hamamelidaceae) in Response to Climate Change after the Last Interglacial Period. *Forests* **2020**, *11*, 434. [CrossRef]
44. Vanagas, G. Receiver operating characteristic curves and comparison of cardiac surgery risk stratification systems. *Interact. Cardiovasc. Thorac. Surg.* **2004**, *3*, 319–322. [CrossRef]
45. Elith, J.; Kearney, M.; Phillips, S. The art of modelling range-shifting species. *Methods Ecol. Evol.* **2010**, *1*, 330–342. [CrossRef]
46. Parmesan, C. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **2006**, *37*, 637–669. [CrossRef]
47. Hanson, P.J.; Weltzin, J.F. Drought disturbance from climate change: Response of United States forests. *Sci. Total. Environ.* **2000**, *262*, 205–220. [CrossRef] [PubMed]
48. Gao, L.Y.; Huang, X.R.; Xi, Y.Y.; Li, J.J.; Ma, K. Analysis on Characteristics of Temporal-spatial Climate Distribution in Sichuan Basin Based on Cloud Model. *J. N. China Univ. Water Resour. Electr. Power* **2017**, *38*, 1–7. [CrossRef]
49. Zhou, P.; Liu, Z.Y. Analysis of Climatic Characteristics and Trend in Typical Regions with the Same Latitude as the Nanling Moutainous Area. *Trop. Geogr.* **2018**, *38*, 299–311. [CrossRef]
50. Xu, W.-B.; Svenning, J.-C.; Chen, G.-K.; Zhang, M.-G.; Huang, J.-H.; Chen, B.; Ordonez, A.; Ma, K.-P. Human activities have opposing effects on distributions of narrow-ranged and widespread plant species in China. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 26674–26681. [CrossRef]
51. Kharuk, V.I.; Ranson, K.; Dvinskaya, M. Evidence of Evergreen Conifer Invasion into Larch Dominated Forests During Recent Decades in Central Siberia. *Eurasian J. For. Res.* **2007**, *10*, 163–171.
52. Ikeda, D.H.; Max, T.L.; Allan, G.J.; Lau, M.K.; Shuster, S.M.; Whitham, T.G. Genetically informed ecological niche models improve climate change predictions. *Glob. Chang. Biol.* **2017**, *23*, 164–176. [CrossRef]