How Climate Change Will Alter the Distribution of Suitable *Dendrobium* Habitats

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To protect endangered species and restore their habitats, it is important to be able to predict their potential geographic distributions. The *Dendrobium* plant is important in traditional Chinese medicine, but urban expansion and over-exploitation have led to a decrease of *Dendrobium* resources. To achieve sustainable development of *Dendrobium* resources, the spatial and temporal distribution of two *Dendrobium* species were systematically analyzed based on the distribution points of *D. moniliforme* (104) and *D. nobile* (87). Maximum entropy modeling (MaxEnt) was used to predict the distribution of suitable habitats for these *Dendrobium* species, both currently and in the future, under different representative concentration pathways (RCPs). Three RCPs included RCP2.6, RCP4.5, and RCP8.5. The results show that *D. moniliforme* and *D. nobile* are widely distributed in the south of China (Anhui, Guangdong, Jiangxi, and Hunan provinces). Worldwide, Japan and North Korea were identified as major distribution areas for *D. moniliforme* and *D. nobile*. Based on the MaxEnt model, the mean diurnal range and the minimum temperature of the coldest month were identified as the most significant bioclimatic variables controlling the distribution of *D. moniliforme* and *D. nobile*. Future climate change will likely result in an increase of suitable habitat areas for *D. moniliforme* (by around 16%), and a decrease for *D. nobile* (by around 1–10%), but climate change is unlikely to have much impact on the distribution of suitable habitats for *D. moniliforme* and *D. nobile* in Japan and North Korea. Based on our findings, measures should be taken to protect these precious medicinal plant resources, and the sites used for the artificial cultivation of *Dendrobium* will need to shift as the climate changes.

Keywords: *Dendrobium*, ArcGIS, MaxEnt, ecologically suitable distributions, climate change

INTRODUCTION

Climate is the most important factor determining the distribution of species on Earth, and changes in species distributions reflect changes in climate (Tanaka et al., 2012; Faleiro et al., 2013; Li et al., 2013). There have been many studies addressing the relationship between climate change and the distributions of the herbs used in traditional Chinese medicine (Szakiel et al., 2011; Li et al., 2015; Guo et al., 2016). *Dendrobium* is the second-largest Orchid genus (∼1,500 species). Although *Dendrobium* species are native to China, Japan, the Philippines, Thailand, and other countries,

they are mainly distributed in the tropical and subtropical regions of Asia and Oceania; there are only 80 species and two varieties of *Dendrobium* in China (Wu et al., 2009; Zheng et al., 2018). The fresh or dried stems of many *Dendrobium* species are one of the most expensive tonics in traditional Chinese medicine, and these tonics are considered a "superior grade" herbal medicine in the ancient text "Shen Nong's Herbal Classic" (Xu et al., 2013). The main chemical components of *Dendrobium* are alkaloids, aromatic compounds, sesquiterpenoids, and polysaccharides, with multiple biological activities, including immunomodulatory, neuroprotective, and anti-tumor effects, with high research and development value (Xu et al., 2013). The world's medicinal *Dendrobium* is almost exclusively sourced from the wild. A huge and persisting market demand has led to the overharvesting of wild *Dendrobium*, which is now endangered. Also, indiscriminate collection is destroying the natural environment that *Dendrobium* depends on.

The climatic conditions of *Dendrobium* are relatively special, and the *Dendrobium* species found differ among regions. Generally, the average annual temperature in the distribution area is 8.5–21.7°C, the annual extreme maximum temperature is up to 35.7°C, the annual extreme minimum temperature is −1.6°C, the optimal temperature in the growing period is 20–30°C, and the average temperature in winter is 1–12.2°C (Baker and Baker, 1996; Xiang et al., 2016). Although *Dendrobium* has some resistance to adverse temperatures, the survival of *Dendrobium* is expected to be affected by changing climatic conditions. Therefore, it is important to analyze and evaluate the likely migration and change of *Dendrobium* growing areas under climate change. Determining the specific distribution points and population density of species through field sampling information and database sample information is the most important tool we have for determining species distribution and habitat. However, it is difficult to objectively measure species distributions and to make reasonable predictions about future species distributions and habitat conditions.

In recent years, species distribution models based on geographic information systems and ecological principles have been widely used in efforts to predict the potential distribution of species. Maximum entropy (MaxEnt), genetic algorithm for rule-set production (GARP), artificial neural network (ANN), species distribution models (SDM), and generalized additive model (GAM) approaches have been used to study the distribution of wild plants under current and future climatic conditions (Raimundo et al., 2007; Haverkost et al., 2010; Tanaka et al., 2012; De Souza and De Marco, 2014; Motloung et al., 2014). MaxEnt is a habitat suitability model based on a niche principle, where species distribution data and environmental data are used to analyze the distribution of species at maximum entropy (Remya et al., 2015). Compared with other niche models, MaxEnt is most robust when relatively few distribution points are available, and because of this, MaxEnt has been widely used by scholars throughout the world (Elith et al., 2006; Phillips et al., 2006; Petitpierre et al., 2012; Zhang M.G. et al., 2016).

Many scholars have studied the relationship between environmental factors (climate and soil) and the potential distribution of *Dendrobium* plants (Khanum et al., 2013; Yang

et al., 2013). However, most current *Dendrobium* research is focused on artificial cultivation, genomics, pharmacology, clinical application, and extraction of chemical components (Teixeira da Silva et al., 2016; Cheng et al., 2019; Yuan et al., 2020). There have been few attempts to describe the distribution of suitable *Dendrobium* habitats, or to predict how future climate is likely to affect this. To address this, here we describe the distribution of two representative *Dendrobium* species (*D. moniliforme* and *D. nobile*) and predict potentially suitable habitats for these species, for both current and under future climate change scenarios. This will provide a theoretical basis for the protection and reasonable introduction of *Dendrobium* resources under current climate conditions. Meanwhile, scientific measures should be taken to protect *Dendrobium* according to the influence of climate factors on the distribution of *Dendrobium* in the future.

MATERIALS AND METHODS

Study Species and Occurrence Data

D. nobile was listed in the Pharmacopia of the People's Republic of China and *D. moniliforme* has a high medicinal value. These two species were planted more widely in the world and have greater potential for promotion and cultivation. So, we selected these two representative species to study the current and future distributions of the *Dendrobium* species. The current distribution of suitable habitats for *D. moniliforme* and *D. nobile* is shown in **Figure 1**. The distribution point records of two different *Dendrobium* species were derived from the Global Biodiversity Information Network Database[1] (GBIF), China Digital Herbarium[2] (CVH), China's eFlora website[3], and the China National Knowledge Infrastructure[4].

To ensure the accuracy of the *Dendrobium* distribution points, the obtained distribution point records were strictly screened. First, we selected the Latin name and accurate latitude and longitude points, eliminating any Latin name errors, and incomplete or repeated latitude and longitude points. Next, for the points with exact place names but no longitude and latitude, this data was gathered using Google Earth[5] 7.0. Ultimately, we gathered 104 distribution points for *D. moniliforme* and 87 distribution points for *D. nobile*. The distribution points data of *Dendrobium* were stored in a.csv format for later use, sorted by species name, longitude, and latitude. ArcGIS 10.5 (Esri, Redlands, CA, United States) and.csv files of the two *Dendrobium* distribution points data were used to map the distribution points of the two *Dendrobium* species. The time span of distribution points in the database was 1930–2018, mainly distributed at 25–50°N and 80–150°E. Considering possible climate change within the early distribution points, we removed the distribution points with earlier recorded times. From the distribution range of the

[1]http://www.gbif.org/
[2]http://www.cvh.org.cn/
[3]http://www.eflora.cn
[4]http://www.cnki.net/
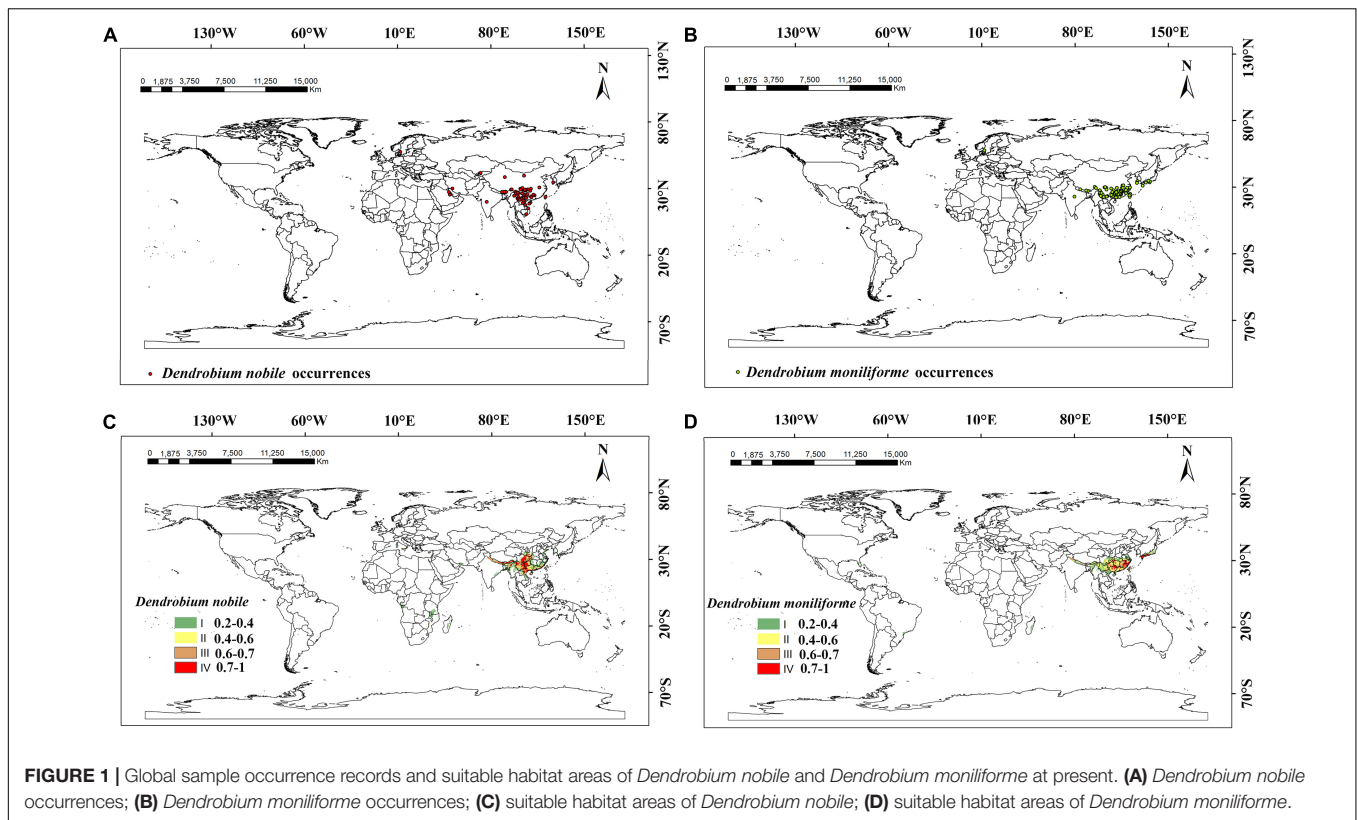[5]http://earth.google.com

FIGURE 1 | Global sample occurrence records and suitable habitat areas of *Dendrobium nobile* and *Dendrobium moniliforme* at present. **(A)** *Dendrobium nobile* occurrences; **(B)** *Dendrobium moniliforme* occurrences; **(C)** suitable habitat areas of *Dendrobium nobile*; **(D)** suitable habitat areas of *Dendrobium moniliforme*.

occurrence data, China and Japan have a more concentrated set of distribution points, while India, Iran, and Saudi Arabia also have small numbers of distribution points.

Predictor Environmental Variables

Nineteen bioclimatic variables (bio01–bio19) of current times and the future (the 2050s and 2070s) were downloaded from the Global Climate Databases[6] with 5-min spatial resolution (**Table 1**). Biological variables came from three different representative concentration pathways (RCPs), including RCP2.6, RCP4.5, and RCP8.5, which represented low, moderate, and high greenhouse gas emission scenarios, respectively. The elevation data (ALT) of topographic variables extracted using ArcGIS 10.5 (Esri, Redlands, CA, United States) were derived from the National Geophysical Data Center[7]. As the coordinate system, we used WGS84, which includes indicators such as annual average, seasonal average and monthly average temperature/humidity, annual average sunshine, and annual average precipitation. CCSM4 is an efficient global climate tool for the simulation of future climatic conditions, which has been thoroughly evaluated in China and successfully applied to predict the influence of future climatic changes on the distribution of plant species in similar environments (Vertenstein et al., 2010; Meehl et al., 2012, 2013; Li et al., 2020; Yan et al., 2020). Four RCPs were established, ranging from RCP 2.6 (aggressive mitigation/lowest emission scenario) to

RCP 8.5 (highest emission scenario) in the fifth report of the Intergovernmental Panel on Climate Change (IPCC), and the RCP2.6, RCP 4.5, and RCP 8.5 scenarios were selected to model the prospective potential distribution of *Dendrobium* under a maximum emissions scenario hypothesis (Li et al., 2020).

The prediction result of the MaxEnt model will be over-fitted due to the collinearity between various ecological factors (Graham, 2003). To exclude the over-fitting of model prediction results, the Spearman coefficient method is used to detect the correlation of 20 ecological factors (**Figure 2**). If the correlation coefficient of the two factors is greater than or equal to 0.8, the factors with a contribution rate are retained, and factors with a correlation coefficient of less than 0.8 are retained (Zhang H. et al., 2016). Based on the analysis of the MaxEnt model and the Spearman coefficient method, this study ultimately selected eight and ten environmental factors for *D. moniliforme* and *D. nobile*, respectively, and these data were used to map the potential distributions of *Dendrobium* and identify the key variables. The digital elevation model was resampled using ArcGIS 10.5 (Esri, Redlands, CA, United States) to make the spatial resolution the same as the 19 bioclimatic variables. All variables were converted into the ASCII format via ArcGIS 10.5 (Esri, Redlands, CA, United States) for use with the MaxEnt software.

Maximum Information Entropy Modeling Analysis

At present, the MaxEnt model has successfully predicted the potential distribution areas of various plants and achieved

TABLE 1 | Selected environmental variables in the MaxEnt model and their units in predicting the current and future distribution of *Dendrobium nobile* and *Dendrobium moniliforme*.
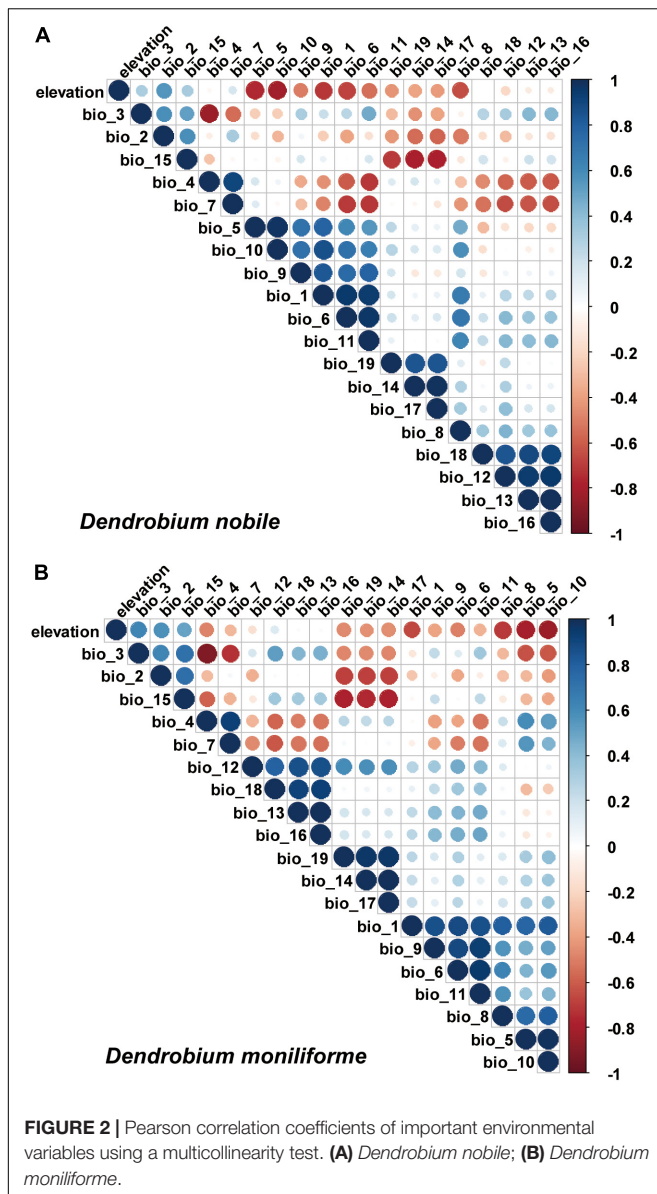
Type	Variables	Description	Units
Topographic variables	Elevation	Elevation	M
Bioclimatic variables	Bio1	Annual mean temperature	°C
	Bio2	Mean diurnal range [mean of monthly (max temp − min temp)] (°C)	°C
	Bio3	Isothermality (Bio2/Bio7) (× 100)	–
	Bio4	Temperature seasonality (standard deviation × 100) (coefficient of variation)	°C
	Bio5	Maximum temperature of warmest month	°C
	Bio6	Minimum temperature of coldest month	°C
	Bio7	Temperature annual range (bio5-bio6)	°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 (coefficient of variation)	–
	Bio16	Precipitation of wettest quarter	mm
	Bio17	Precipitation of driest quarter	mm
	Bio18	Precipitation of warmest quarter	mm
	Bio19	Precipitation of coldest quarter	mm

good results based on the sampling point information of the species distribution and environmental variables (Haverkost et al., 2010; De Souza and De Marco, 2014; Motloung et al., 2014; Zhang et al., 2018). So, in this study, we intend to use the MaxEnt model for analysis. After analyzing the contribution of environmental factors to the growth and distribution of *Dendrobium* with the MaxEnt 3.4.1 software, a MaxEnt prediction model based on the actual distribution records and ecological variables was established. The overall probability of *Dendrobium* occurrence was calculated, and its suitable habitat area was predicted. The potentially suitable habitats of the two *Dendrobium* species at current and future periods in the world were obtained using ArcGIS 10.5 (Esri, Redlands, CA, United States). The specific operation method is as follows: first, the selected ecological variables and the occurrence data of *D. moniliforme* and *D. nobile* were respectively optimized by R, the performance of different models was evaluated to obtain the best-fitting model using the R package "ENMeval" and the package "dismo" was used to establish a model of species distribution (Hijmans et al., 2013; Muscarella et al., 2014). The features and regularization multiplier for the MaxEnt model were obtained by optimizing relevant data through R. Next, the ecological variables and the occurrence data were loaded into the MaxEnt model; 75% of the location data were used for training, and the remaining 25% were used to test the predictive ability of the model. The model ran either 500 iterations of these processes or continued until a convergence threshold of 0.00001 was met. The logistic output was chosen as an estimate of the probability of the presence conditioned by the ecological variables, per grid cell. The features and regularization multiplier were set according to

the optimization result of R; other parameters were kept as the default.

Modeling Evaluation

The accuracy of the prediction of the MaxEnt model under different conditions needs to be quantified by calculating the area under the receiver operating characteristic (ROC) curve (AUC) (Lobo et al., 2008). AUC values below 0.7 were considered as poor; values between 0.7 and 0.9 were moderate, and >0.9 were considered as high (Franklin, 2010). The Jackknife method is an analytical method to evaluate the reliability of the model, and the ROC curve of the knife-cut method is a commonly used model in the evaluation of the potential distribution model of species (Dorfman et al., 1992; Townsend Peterson et al., 2007). A larger value of the AUC indicates a more accurate prediction. These values are typically between 0.8 and 0.9, and values between 0.9 to 1.0 are considered very good (Swets, 1988). There are many ways to divide suitable habitat areas when studying the relationship between the environments of plant-suitable habitat areas. To do this, we synthesized the existence probability of *Dendrobium* and used an artificial classification method with a good division effect to divide the suitable habitat area of *Dendrobium* into four levels: high habitat suitability (existence probability of 0.7–1), moderate-high habitat suitability (existence probability of 0.6–0.7), moderate habitat suitability (existence probability of 0.4–0.6), and low habitat suitability (existence probability of 0.2–0.4) (Yang et al., 2013). In the climate factor response map generated by the knife-cut method, the resulting values with a probability of existence greater than 0.5 were taken as the most suitable ecological factor range for the species in this study (Hemery et al., 2016).

FIGURE 2 | Pearson correlation coefficients of important environmental variables using a multicollinearity test. **(A)** *Dendrobium nobile*; **(B)** *Dendrobium moniliforme*.

RESULTS

Model Performance for *Dendrobium* Species

At present, ROC analysis is recognized as the best evaluation index for diagnostic tests and the area under the ROC curve (AUC value) is used to measure the accuracy of model prediction (Wang et al., 2007; Peterson et al., 2008; Yuan et al., 2015). The larger the AUC value, the larger the true positive rate and the smaller the false positive rate, which means that the prediction result of the model is more accurate. When the AUC value is greater than 0.8, the accuracy of the model prediction is high. When the AUC value is greater than 0.9, the model prediction area matches the actual species distribution and has excellent performance (Howell et al., 2011; Pourghasemi et al., 2017).
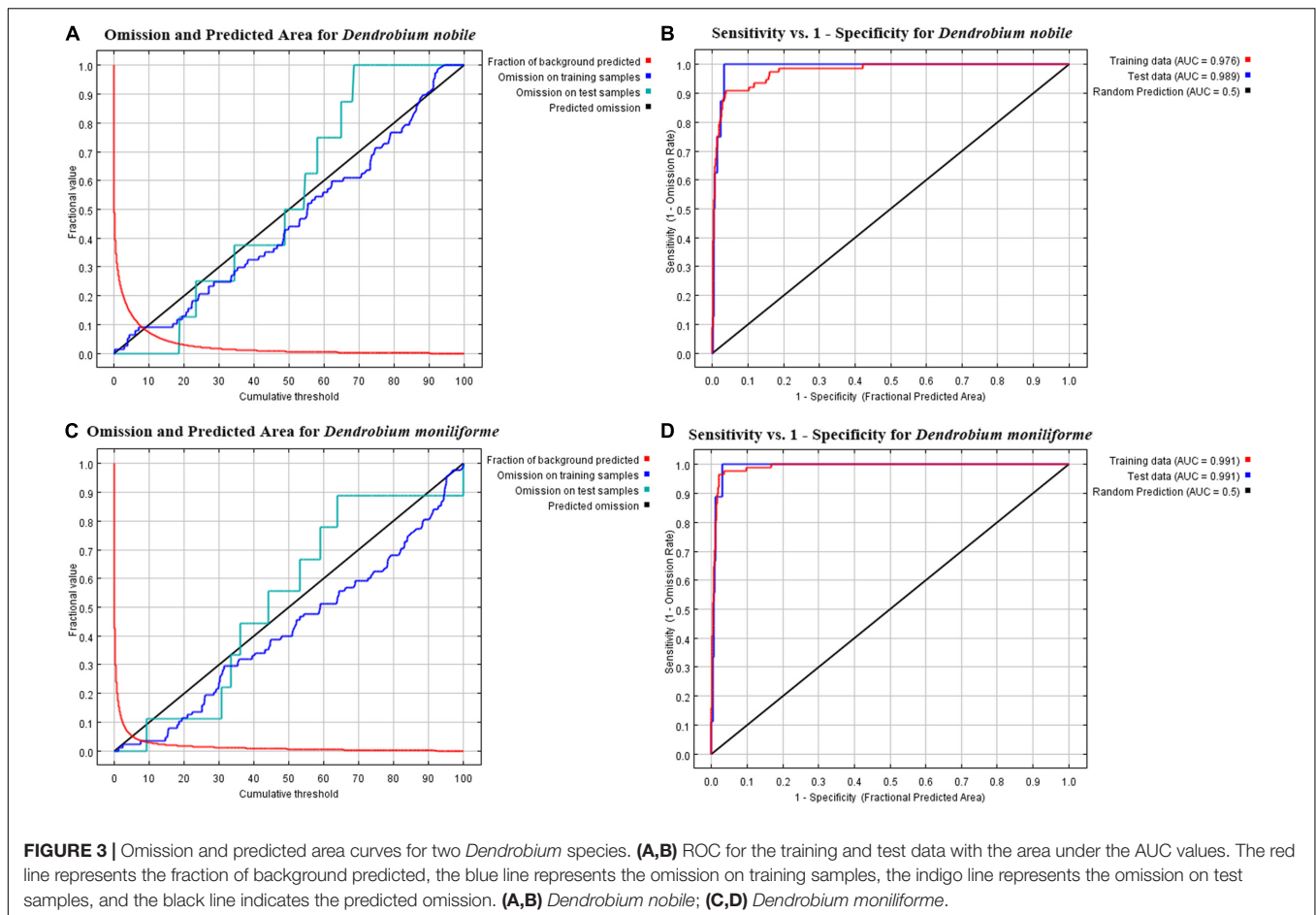
The AUC results of the MaxEnt model are shown in **Figure 3**. In *D. nobile*, the AUC value of the training set reached 0.976, and the AUC value of the test set reached 0.989 in the current situation. In *D. moniliforme*, the AUC values of both the training and testing sets reached 0.991 in the current situation. In the future (the 2050s and 2070s), under different greenhouse gas emission models, the AUC values of training and testing of the *D. nobile* and *D. moniliforme* sets both exceeded 0.975. These results show that the predicted distribution area in the current period was highly consistent with the natural distribution area, and the MaxEnt model has high credibility and accuracy in calculating suitable habitat areas for *Dendrobium* for current and various future periods.

Environments That Constrain the Model

The MaxEnt model obtains the contribution rate of each ecological factor through iterative calculation and normalization. It essentially provides a measure of the relative importance of each ecological variable, and the greater the contribution rate, the greater the impact on plant growth and distribution. The Jackknife test can analyze each environmental variable with a knife-cut method, and can distinguish that different variables have different effects on the potential distribution area of *Dendrobium* plants (**Figure 4**). The relative importance of the various ecological variables showed that the mean diurnal range (bio2), temperature seasonality (bio4), minimum temperature of the coldest month (bio6), annual precipitation (bio12), precipitation of the driest month (bio14), precipitation seasonality (bio15), precipitation of the warmest quarter (bio18), and elevation were important factors in predicting the geographic distribution for *D. moniliforme*, and that the cumulative contribution rate of temperature seasonality (bio4), minimum temperature of the coldest month (bio6), and precipitation of the warmest quarter (bio18) reached 77.3% (**Table 2**).

Similarly, among the ten ecological variables that are highly correlated with the geographical distribution of *D. nobile*, the cumulative contribution rate of the mean diurnal range (bio2), minimum temperature of the coldest month (bio6), and precipitation seasonality (bio15) reached 69.8% (**Table 2**). As shown in **Figures 5** and **6**, the response curves of the distribution model of *D. nobile* and *D. moniliforme* indicated a high probability of occurrence (probability of presence >0.6) of this species in these regions. In the current period, *D. moniliforme* and *D. nobile* are both greatly affected by the minimum temperature of the coldest month (bio6), and its effect on *D. nobile* is greater than other ecological factors, which indicates that the two *Dendrobium* species have greater sensitivity to low temperatures. The difference is that the largest ecological factor affecting *D. moniliforme* is the precipitation of the warmest quarter (bio18), which indicates that the two *Dendrobium* species of the same genus have different environmental requirements.

In the future (the 2050s and 2070s), under different greenhouse gas emission scenarios, the contribution rate of ecological factors affecting the growth and distribution of *D. moniliforme* and *D. nobile* will change to some extent. With the change of time, space, and climate, some ecological factors gradually increase their contribution rate to *Dendrobium*, while

FIGURE 3 | Omission and predicted area curves for two *Dendrobium* species. **(A,B)** ROC for the training and test data with the area under the AUC values. The red line represents the fraction of background predicted, the blue line represents the omission on training samples, the indigo line represents the omission on test samples, and the black line indicates the predicted omission. **(A,B)** *Dendrobium nobile*; **(C,D)** *Dendrobium moniliforme*.

some ecological factors have a smaller impact on *Dendrobium*, which indicates that *Dendrobium* is affected by different factors in different situations, and also has a certain ecological adaptability under climate change.

Predicting the Distribution of Suitable Habitats Under Current Conditions

The suitable habitats (from high suitability to low suitability) of *D. moniliforme* and *D. nobile* are mainly distributed in the southeastern and southwestern regions of China and the regions around the Tibetan plateau, including Guangdong, Guangxi, Yunnan, Guizhou, and Taiwan. At the same time, *D. moniliforme* is also distributed in the southern islands of Japan, the coast of South Korea, eastern and northeastern Australia, the eastern coast of Canada, eastern Madagascar, and western Norway. Compared with *D. moniliforme*, the suitable habitat areas of *D. nobile* in southern Japan and western Canada are significantly reduced, which indicates that these areas did not meet the climatic conditions required for *D. nobile* to grow. In contrast, suitable habitat areas for *D. nobile* exist on the Mediterranean coast and parts of Mozambique and Zimbabwe and the distribution area of *D. nobile* in China is significantly larger than *D. moniliforme*. According to the actual distribution and prediction results of *Dendrobium*, the suitable habitat areas

of *D. nobile* and *D. moniliforme* are basically consistent with the current actual distribution area and are mainly concentrated in the coastal areas of all continents, which indicates the accuracy of the prediction results and the importance of temperature and moisture to the growth and distribution of *Dendrobium*.

Predicted Future Potential Species Distribution

The analysis and prediction of the potential suitable distribution of *D. nobile* and *D. moniliforme* under the three greenhouse gas emission scenarios (RCP 2.6, RCP 4.5, and RCP 8.5) in the 2050s and 2070s are shown in **Figures 7** and **8**. Under the RCP 2.6 and RCP 4.5 greenhouse gas emission scenarios, the suitable habitat areas for *D. moniliforme* will be mainly concentrated in central and eastern Zhejiang, northern Fujian, northwestern Guangdong, Guangxi, Taiwan, and most of Guizhou province. It is also suitable for growth in southern Japan, Canada, and the west coast of Sweden. Under RCP 8.5, the suitable habitat areas for *D. moniliforme* will be expanded to Anhui, Jiangxi, southeastern Shanxi Province, and parts of Chongqing. Compared with RCP 2.6 and RCP 4.5, the suitable habitat area of *D. moniliforme* in Guizhou Province will be greatly reduced, which indicates that the climatic conditions of Guizhou Province in the 2050s will be unsuitable for the growth of
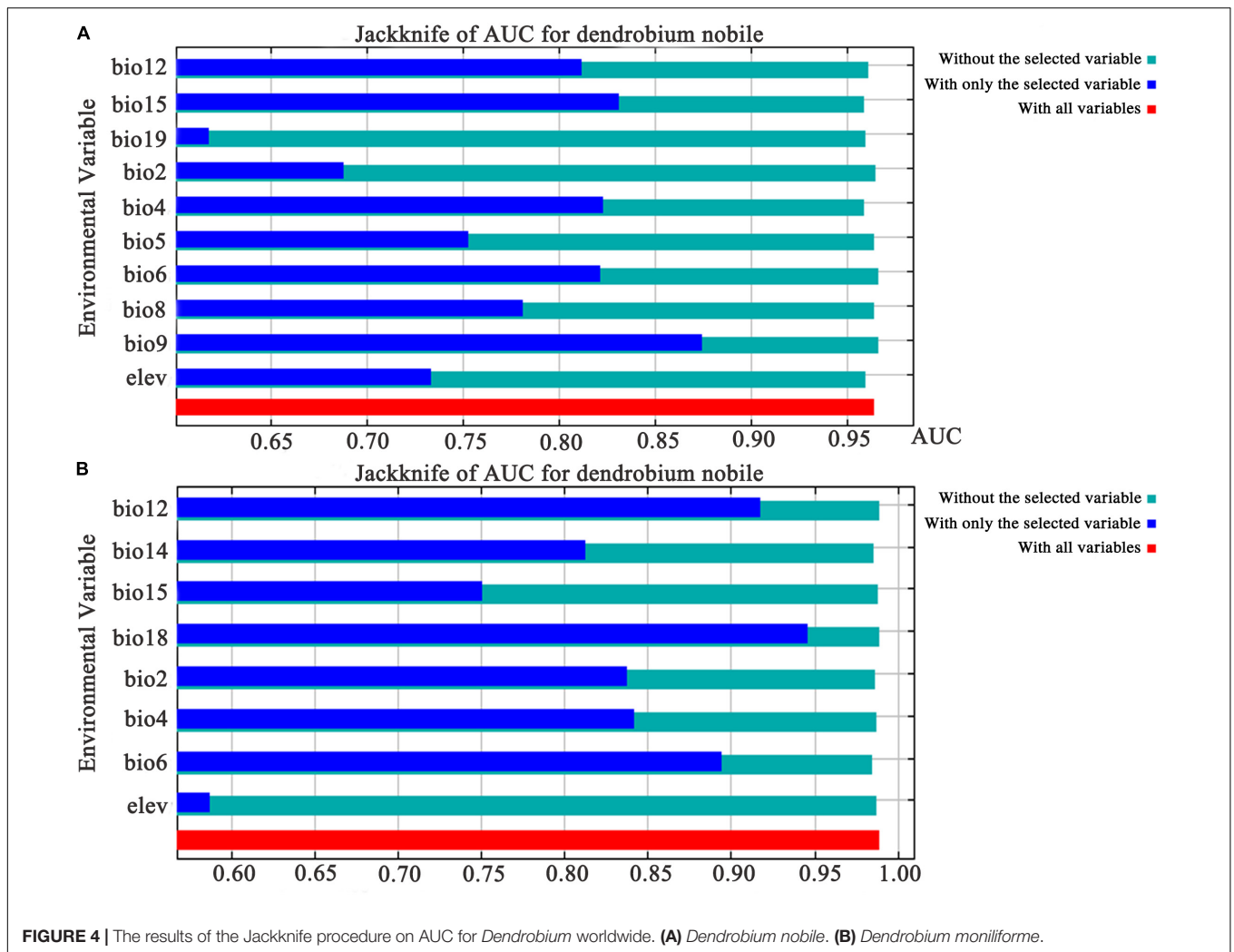
FIGURE 4 | The results of the Jackknife procedure on AUC for *Dendrobium* worldwide. **(A)** *Dendrobium nobile*. **(B)** *Dendrobium moniliforme*.

D. moniliforme under RCP 8.5 conditions. The distribution area of *D. moniliforme* is roughly the same under the three greenhouse gas emission scenarios in the 2070s. Compared with the 2050s, the suitable area in the coastal areas of eastern Fujian and Zhejiang and parts of Hubei have been significantly reduced. In the long-term, the suitable habitat area of *D. moniliforme* will be continuously reduced in the future, and is predicted to be reduced by 16% by the 2070s (**Table 3**). Therefore, it is expected that *D. moniliforme* resources will face greater challenges in the future.

The potential future distribution of habitats suitable for *D. nobile* was analyzed. These predictions were largely under the three tested greenhouse gas emission scenarios. In China, *D. nobile* will be mainly distributed in Guangxi, Fujian, Guizhou, Chongqing, southwestern Taiwan, east coast of Guangdong, and the southern Tibet Plateau of Qinghai Province. Worldwide, it is distributed mainly in a small part of the Mediterranean coast, Zimbabwe, and Zambia. Compared with the 2050s, the area of suitable habitats for *D. nobile* in the 2070s period will continue to expand. Under RCP4.5, the area suitable for *D. nobile* is expected to increase by 10% (**Table 3**).

Dendrobium nobile and *D. moniliforme* show different changing trends in the context of future climate change. During the period of the 2050s, the area of suitable habitats of *D. nobile* and *D. moniliforme* changed under different greenhouse gas emission patterns, but generally made steady progress, which indicates that the two *Dendrobium* species have some adaptability to climate change. In the 2070s, the suitable habitat area of *D. nobile* will continue to increase, but that of *D. moniliforme* will continue to decrease, indicating that *D. nobile* has better adaptability to environmental changes than *D. moniliforme* under future climate change scenarios.

DISCUSSION

Significance of Model Predictions and Comparison With Previously Recorded Distributions

Environmental factors affect the growth, quality, and efficacy of Chinese herbal medicines (Grimm et al., 2008; Yang et al., 2011;

TABLE 2 | Relative contribution of selected environmental variables in the MaxEnt model for two *Dendrobium* species.

Variable	Contribution for *D. moniliforme* (%)						
	Current	2050-2.6	2050-4.5	2050-8.5	2070-2.6	2070-4.5	2070-8.5
Bio2	5.4	5.9	18.8	1.7	16.7	18.3	18.5
Bio4	14.8	13.7	1.7	14.9	2.1	1.9	2.2
Bio6	14.5	15.3	35.5	3.8	34.6	35.1	34.9
Bio12	4.3	5.3	0.4	4	0.8	0.3	0.8
Bio14	3.5	2.4	1.3	2.9	1.5	1.8	1.6
Bio15	4.5	5.2	5.6	6	5.2	7	8.3
Bio18	48	48.9	34.9	66	37.4	34	32.5
Elevation	4.9	3.2	1.7	0.6	1.6	1.7	1.3

Variable	Contribution for *D. nobile* (%)						
	Current	2050-2.6	2050-4.5	2050-8.5	2070-2.6	2070-4.5	2070-8.5
Bio2	22.9	21.4	22.5	20.3	21.8	12.2	7.9
Bio4	2.7	2.4	2.2	2.9	2.4	15.6	18.3
Bio5	0.6	0.4	0.4	0.6	0.4	3.1	4
Bio6	32.8	31.3	30.8	31.8	31.3	18.3	9.7
Bio8	4.8	3.3	3.5	2.8	3.4	0.7	0.2
Bio9	2.3	1.4	0.7	0.9	0.6	1.1	3.1
Bio12	5.4	9.1	9.3	10.5	8.8	22	25.2
Bio15	14.1	19	17.7	18.8	19.3	15.1	19.4
Bio19	4.2	3.6	4.1	4.1	3.8	4.8	5.6
Elevation	10.2	8	8.8	7.2	8.1	7.2	6.4

Huang et al., 2012; Shang et al., 2015). The overexploitation of wild Chinese herbal medicines damages the environment and leads to shortages (Zhang and Li, 2008; Wu et al., 2011). As a traditional Chinese herbal medicine with great medicinal value, *Dendrobium* needs further development and utilization (Bi et al., 2004; Shao et al., 2004; Xu and Wang, 2005; Zhang et al., 2007; Hsieh et al., 2008; Ng et al., 2012; Pan et al., 2014). However, the destruction of the ecological environment and excessive excavation are increasing the strain on the wild resources of *Dendrobium* and shrinking the area available for its growth (He et al., 2008). Therefore, to protect *Dendrobium* supplies, it will be important to understand where it can be grown, both now and in the future (Kolanowska and Konowalik, 2014; Jalal, 2019). In recent years, model methods have been continuously optimized in practice. The MaxEnt model has been widely used as a model to predict the potential geographical distribution of species, and has achieved good prediction results.

As a machine learning model, the MaxEnt model does not require prior data conversion and the elimination of outliers (Boutaba et al., 2018; Liu et al., 2018; Kalinski, 2019). It is also possible to combine data from multiple measurement scales without making statistical assumptions, thus helping to stimulate natural phenomena with non-linear relationships (Phillips, 2005; Kramer-Schadt et al., 2013; Phillips et al., 2017). In recent years, the MaxEnt model has been widely used in the analysis of invasive alien species and the study of the suitability of Chinese medicinal materials, and has achieved good prediction results (Fan et al., 2019; Huang et al., 2019; Tang et al., 2019; Wei et al., 2019). Although the MaxEnt model has some shortcomings, it has

high performance and accuracy in modeling, high operational modeling capabilities, and a very friendly interactive interface. Because of these advantages, the MaxEnt model is becoming increasingly and more widely used (Warren and Seifert, 2011; Renner and Warton, 2013; Yuan et al., 2015; West et al., 2016; Yi et al., 2016).

Given the pressures on *Dendrobium* resources and the importance of estimating the current and future distributions of suitable *Dendrobium* habitats, the MaxEnt model is well-suited to this task. To our knowledge, this is the first time that the MaxEnt model and ArcGIS 10.5 (Esri, Redlands, CA, United States) have been used to model the distribution of *Dendrobium* species. According to available records, *Dendrobium* is mainly distributed in tropical and subtropical regions, such as southeast and southwest China, the areas surrounding the Qinghai-Tibet Plateau, Japan, India, Nepal, Sikkim, Bhutan, Myanmar, Thailand, Laos, Vietnam, and Europe and America (Baker and Baker, 1996; Lo et al., 2004; Zhang et al., 2005; Asahina et al., 2010). The current simulation results of *Dendrobium* are basically the same as the actual distribution, which also illustrates the accuracy of the MaxEnt prediction results from another aspect.

Prospective Change of Distribution Ranges in the Future

Dendrobium is a perennial epiphytic herb with unique habitats and strict microclimate environmental requirements (Ding et al., 2018). *Dendrobium* is mainly distributed in warm and cool environments with an average annual temperature of 18–23°C,
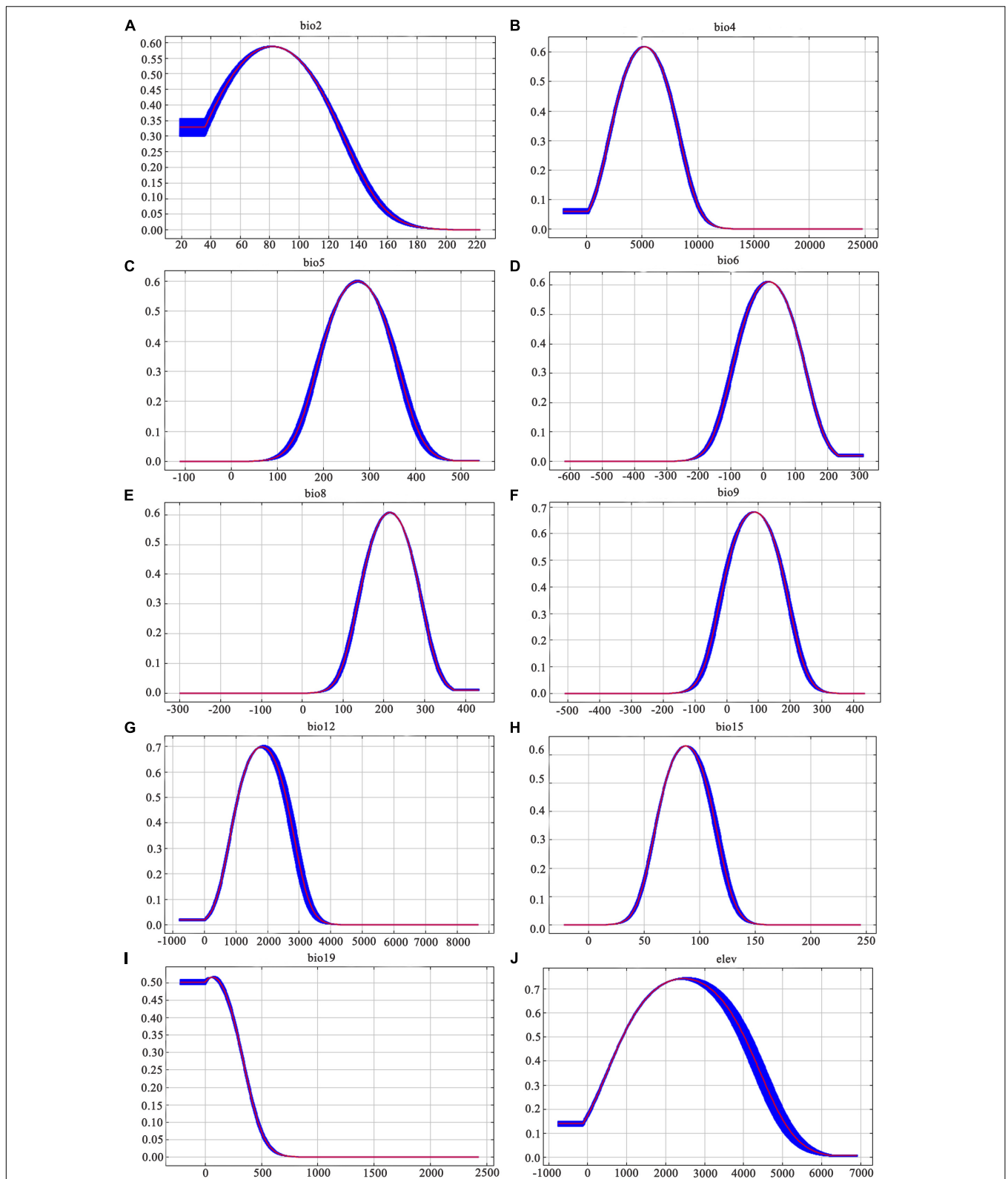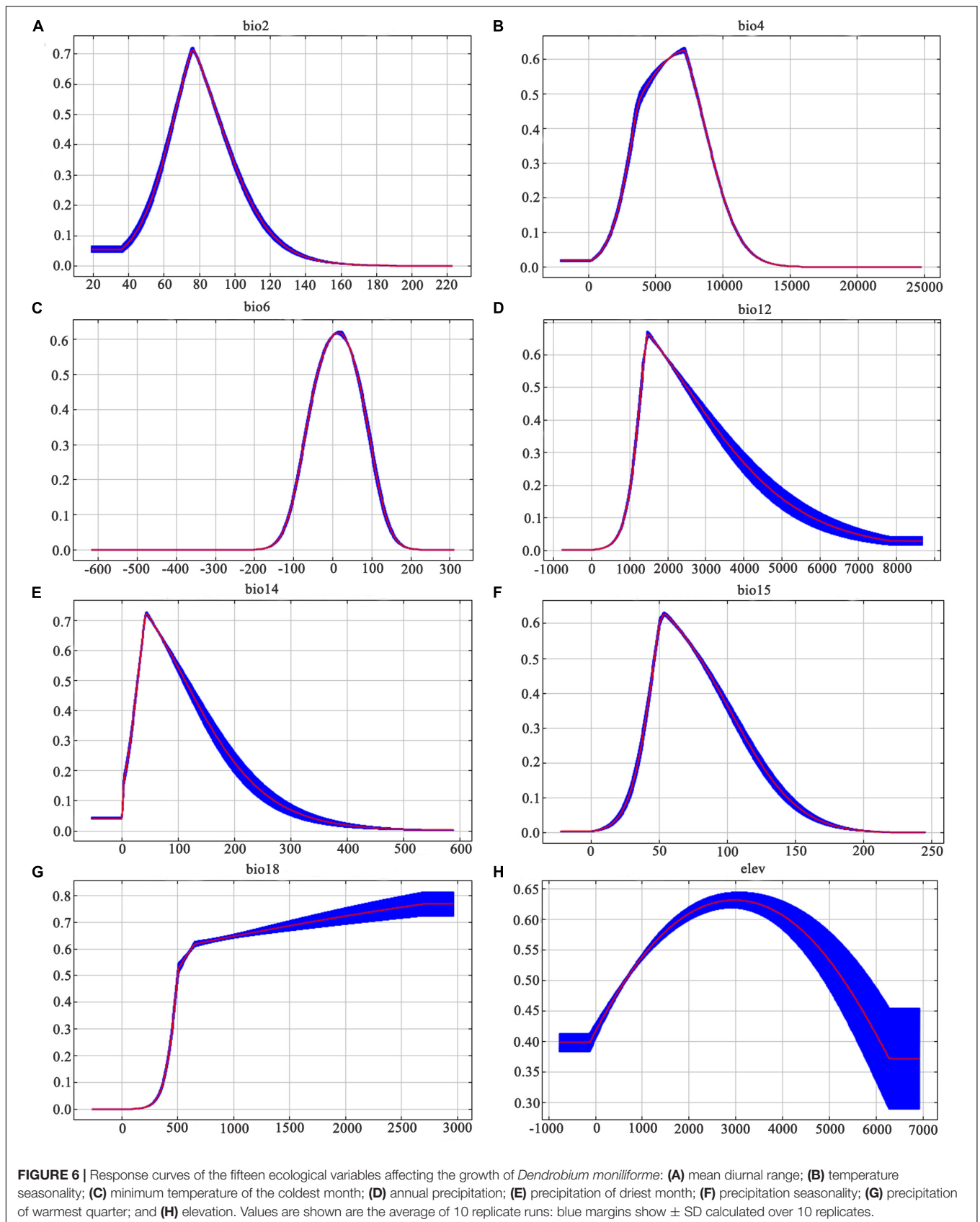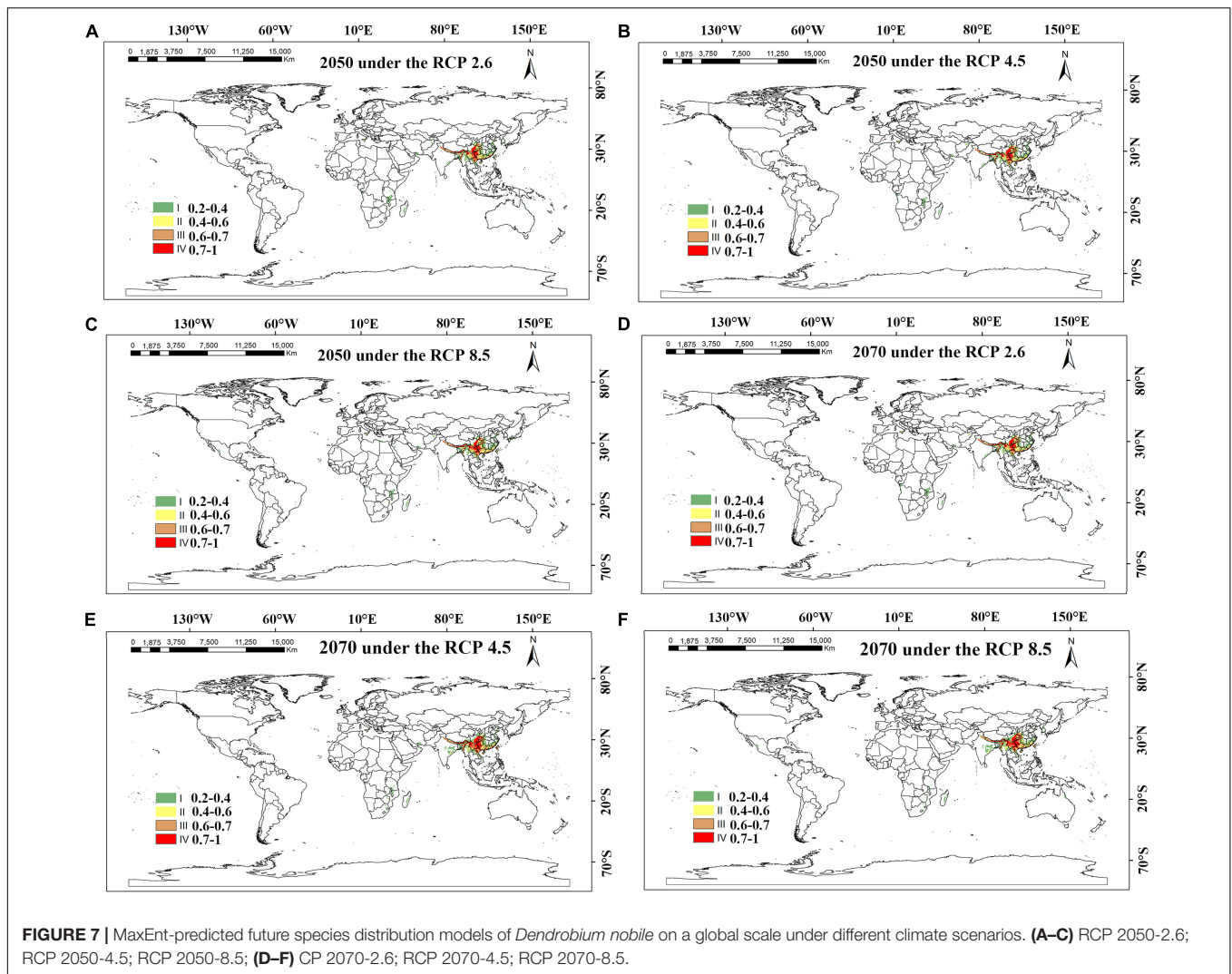
FIGURE 5 | Response curves of the ten ecological variables affecting the growth of *Dendrobium nobile*: **(A)** mean diurnal range; **(B)** temperature seasonality; **(C)** maximum temperature of warmest month; **(D)** minimum temperature of the coldest month; **(E)** mean temperature of the wettest quarter; **(F)** mean temperature of driest quarter; **(G)** annual precipitation; **(H)** precipitation seasonality; **(I)** precipitation of coldest quarter; and **(J)** elevation. Values shown are the average of 10 replicate runs: blue margins show ± SD calculated over ten replicates.

FIGURE 6 | Response curves of the fifteen ecological variables affecting the growth of *Dendrobium moniliforme*: **(A)** mean diurnal range; **(B)** temperature seasonality; **(C)** minimum temperature of the coldest month; **(D)** annual precipitation; **(E)** precipitation of driest month; **(F)** precipitation seasonality; **(G)** precipitation of warmest quarter; and **(H)** elevation. Values are shown are the average of 10 replicate runs: blue margins show ± SD calculated over 10 replicates.

FIGURE 7 | MaxEnt-predicted future species distribution models of *Dendrobium nobile* on a global scale under different climate scenarios. **(A–C)** RCP 2050-2.6; RCP 2050-4.5; RCP 2050-8.5; **(D–F)** CP 2070-2.6; RCP 2070-4.5; RCP 2070-8.5.
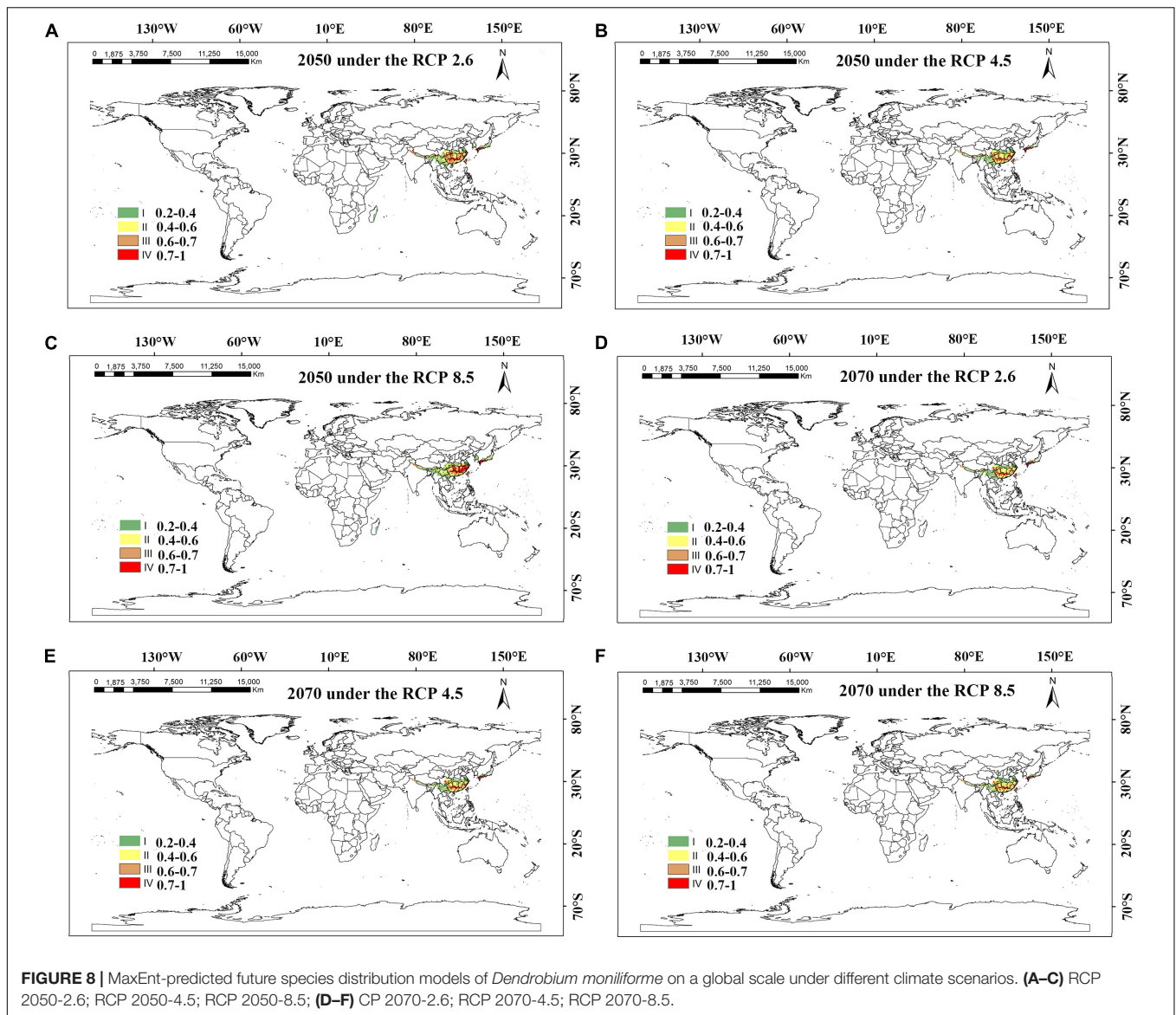
annual precipitation of 100–1200 mm, and relative air humidity of more than 80% (Wood, 2006; Hao L.L. et al., 2012; Sun et al., 2018). Strictly limited by water, wild *Dendrobium* has a low reproduction rate, poor natural regeneration ability, slow growth, and a narrow distribution range (Hu, 1970; Dressler, 1993; Ng et al., 2012; Xu et al., 2013). Orchidacea plants have higher richness at higher temperatures and are more stable in humid regions, which decrease with increasing latitude, indicating that the geographical distribution of orchidaceous plants is closely related to climate factors, such as precipitation and temperature (Teng et al., 2016).

The MaxEnt prediction results show that, at present, *D. nobile* is mainly distributed in southeastern and southwestern China, northern India and southeastern Asia, southeastern Africa, the Mediterranean coast, and the south coast of South Korea, and Japan. Some inland areas of India will be suitable for its survival under future climate change conditions. Unlike *D. nobile*, the current distribution of *D. moniliforme* is mainly concentrated in China, South Korea, and Japan, and *D. moniliforme* is absent from regions outside of Asia. We predict that the distribution

area of *D. moniliforme* is unlikely to change much in the future, but also predict that the fitness of *D. moniliforme* will decrease as the climate changes. The predictions suggest that *D. nobile* and *D. moniliforme* have different environmental adaptabilities. The impact of climate change on plant growth and distribution is complex and multifaceted, leading to differences in the distribution and area of plants in suitable habitats in response to climate change (Qin et al., 2015; Cao et al., 2016; Tang et al., 2017; Li et al., 2020).

Li et al. (2019) that predicted the future suitable habitats for *Tuber mustard*, the predicted area of suitable habitats was increased, but were different in comparison between the 2050s and 2070s. The distribution areas of the two species of *Dendrobium* are mainly concentrated in the coastal areas of tropical and subtropical regions, which is consistent with the literature (Zhang et al., 2005; Xiang et al., 2013). The distribution and planting of *Orchidacea* plants in India have been studied, with the authors reporting that India has climatic conditions suitable for the growth of orchid plants (Jennings, 1875). There are also related studies on the distribution of *Dendrobium* in Japan,

FIGURE 8 | MaxEnt-predicted future species distribution models of *Dendrobium moniliforme* on a global scale under different climate scenarios. **(A–C)** RCP 2050-2.6; RCP 2050-4.5; RCP 2050-8.5; **(D–F)** CP 2070-2.6; RCP 2070-4.5; RCP 2070-8.5.

Korea, Southeast Asia, and other countries and regions, which are consistent with the results of our MaxEnt prediction (Ichihashi, 1997; Lavarack et al., 2000; Kim et al., 2015). But findings on the seasonal flowering of *Dendrobium* in Hawaii is inconsistent with the distribution area of our simulation results, which might be related to the choice of climate variables (Paull et al., 1995).

In summary, the two *Dendrobium* distribution areas are concentrated in the coastal areas of tropical and subtropical areas, and the warm and humid air from the ocean provides sufficient moisture for these areas (Sarntinoranont and Wannakrairoj, 2010; Li et al., 2017). Compared with inland areas, the coastal areas have high winter temperatures and low summer temperatures, and the daily and monthly changes in temperature differences are relatively small, providing suitable climate conditions for the growth of *Dendrobium* leaves and flowers (He et al., 1998). The greater silicon elements in coastal areas might also benefit *Dendrobium* species by improving the photosynthetic

capacity and drought tolerance (Carvalho et al., 2013; Reiners Carvalho et al., 2013). As an important distribution area with more than 70 *Dendrobium* species, China should rationally develop wild *Dendrobium* resources based on the suitable habitat data presented here, and artificial cultivation should be strengthened to meet growing demand. It might also be beneficial to attempt to cultivate *Dendrobium* in the humid and warm coastal areas of all continents, such as the west coast of North America and the east coast of Africa, especially *D. nobile*, which has relatively better adaptability to environmental change.

Environmental Variables Affecting the Geographical Distribution of *Dendrobium*

The suitable habitat area of *D. moniliforme* in China will decrease as the temperature rises, and the area of *D. nobile* will gradually increase, which shows that the impact of climate change on

TABLE 3 | Suitable habitat area under various climate scenarios (km^2).

Dendrobium nobile	Level	0.2–0.4	0.4–0.6	0.6–0.7	0.7–1	Total	Percentage of increase or decrease in the distribution area
	Current	166.944	78.000	42.500	70.000	357.444	
	RCP2.6-2050	165.583	84.250	42.722	68.111	360.666	0.90%
	RCP4.5-2050	159.583	83.528	41.528	69.861	354.500	−0.82%
	RCP8.5-2050	165.417	86.528	44.250	72.222	368.417	3.07%
	RCP2.6-2070	164.167	85.806	43.139	69.222	362.334	1.37%
	RCP4.5-2070	170.167	82.778	49.806	93.306	396.057	10.80%
	RCP8.5-2070	150.944	89.333	50.083	90.194	380.554	6.47%
Dendrobium moniliforme	Level	0.2–0.4	0.4–0.6	0.6–0.7	0.7–1	Total	Percentage of increase or decrease in the distribution area
	Current	122.278	114.639	49.639	36.194	322.75	
	RCP2.6-2050	118.639	116.75	65.806	37.861	339.056	5.05%
	RCP4.5-2050	103.917	109.111	47.972	27.167	288.167	−10.72%
	RCP8.5-2050	126.333	109.917	47.333	57.083	340.666	5.55%
	RCP2.6-2070	98.556	103.251	42.472	25.472	269.751	−16.42%
	RCP4.5-2070	100.806	103.139	38.583	24.389	266.917	−17.30%
	RCP8.5-2070	97.972	113.750	40.222	20.944	272.888	−15.45%

the growth and distribution of *Dendrobium* is nuanced and the distribution pattern of these plants will be the result of long-term adaptation to climate (Watson et al., 1998; Macel et al., 2007; Franks et al., 2014; Christmas et al., 2016). Future climate change will surely alter the distribution of plant species throughout the world (Woodward and Williams, 1987; Wu, 2011), and many species will be limited by their inability to adapt to climate change (Leemans and Eickhout, 2004), resulting in instability, decreasing continuity, and increasing fragmentation (Ashcroft et al., 2009). Climate change is expected to reduce the area of suitable habitat for *U. lamellosa*, and this will cause local extinctions (Yan et al., 2018). Related research on other species found that future climate change will affect the distribution of *Sinopodophyllum hexandrum* and *Amygdalus mongolica* adaptive areas, leading to the extinction of these two species (Guo et al., 2014; Ma et al., 2014).

Differences in adaptive ecological factors might account for the opposite trends we report for the suitable habitat areas of *Dendrobium* under future climate conditions. Here we report that the mean diurnal range (bio2), temperature seasonality (bio4), minimum temperature of the cold month (bio6), precipitation seasonality (bio15), and precipitation of the warmest quarter (bio18) have important effects on the growth and distribution of *D. moniliforme* and *D. nobile*. Our analyses suggest that *Dendrobium* can grow at sites with limited variations in temperature, which are warm and humid, and where the rainy and hot periods overlap. This might be mainly related to the effect of the temperature cycle on the flowering of *Dendrobium* and endogenous hormones (Campos and Kerbauy, 2004; Mandal et al., 2004; Sarathum et al., 2010; Davies, 2013). Rainfall will also affect the germination rate of *Dendrobium* seeds (Vendrame et al., 2007; Huehne and Bhinija, 2012).

The leaves and flowers of *Dendrobium Sonia* were studied in response to strong light and high temperature under natural conditions, and it was found that excessive temperature causes damage to the leaves and flowers, and that the flowers were especially sensitive to strong light (He et al., 1998). For annual and biennial *D. nobile*, 25°C is the optimum temperature for plant growth, which has a significant positive impact on its reproductive ability (Ch et al., 2001; Hao L. et al., 2012). For *D. officinale*, photosynthesis is optimal at 30°C, but polysaccharide content was optimal at 20°C (Ai et al., 2010), which likely accounts for why *Dendrobium* is widely distributed in the shade under trees in the forest.

Dendrobium species form unique symbiotic relationships with mycorrhizal fungi (Zhang et al., 2012). Orchid mycorrhizal fungi promote seed germination of *Dendrobium* orchids (Swangmaneecharern et al., 2012). Endophytic fungi affect the growth and polysaccharide and alkaloid content of *D. nobile* by increasing the number of aerial roots (Chen and Guo, 2005). Lanthanum nitrate and orchid mycorrhizal fungi promote the growth of *D. nobile*, including underground and aboveground biomass, and increase the content of active components (Wei et al., 2014). The growth and distribution of mycorrhizal fungi are largely affected by temperature and humidity, and at the same time can improve plant tolerance to temperature changes (Hacskaylo et al., 1965; Koske, 1987; Bunn et al., 2009). Taken together, temperature and moisture affect the distribution of *Dendrobium* either directly, by affecting the growth of *Dendrobium*, or indirectly, by affecting mycorrhizal fungi.

The Application Prospect of MaxEnt in Endangered Species

The MaxEnt model is a model that predicts the spatial distribution and geographic scale of species based on the theory of maximum entropy, which was written using the JAVA language (Phillips et al., 2006; Baldwin, 2009). The MaxEnt model calculates the possible distribution of the target species in the predicted area based on the actual distribution points

of the species and the environmental variables of the species distribution area (Elith et al., 2011). Because the potential distribution area of the predicted species distribution is close to the actual distribution area of the species, the MaxEnt model has been widely used (Cao et al., 2013). In the future, the Maxent model has extensive prospects in predicting the potential distribution and suitability of endangered species. Sustainable and efficient environmental monitoring, scientific protection and management, and restriction of human activities are recommended for endangered plants according to the results of the MaxEnt model. In particular, we should consider the impact of future rapid climate change on the distribution of endangered plant resources, strengthen climate monitoring and genetic diversity protection, and build an early warning system for future climate change.

The sample capacity has an influence on the prediction accuracy and stability of the MaxEnt model. At the same time, there is a lack of research on soil factors and human factors when simulating the future suitable areas of plants with the MaxEnt model. At present, soil science research focuses on a single soil component and a small geographic range, without research on future trends of large-scale soil changes (Walter et al., 2003). Human influences affect the future direction of climate and soil changes, but they are complex and difficult to simulate with models. Another study discussed the impact of climate change on the distribution of plants, but did not discuss the impact of soil and human factors on the future distribution of these plants (Khanum et al., 2013). We believe that the influence of soil and human influences on the distribution of species will be an important direction for future research.

CONCLUSION

To our knowledge, this is the first study to systematically investigate the geographic distribution and present and future potential distributions of *D. moniliforme* and *D. nobile*. *D. moniliforme* and *D. nobile* are abundant in the south of China. In other parts of the world, *D. moniliforme* and *D. nobile* are mainly distributed in parts of Japan and South Korea with tropical and subtropical monsoon climates.

In the future, the coastal areas of multiple continents are expected to become suitable for individual species of *Dendrobium*. In the 2050s and 2070s, we tested three greenhouse gas emission scenarios [high emission (RCP 8.5), medium emission (RCP 4.5), and low emission (RCP 2.6)]. Our model predicts that, under climate warming, the distribution and area

of the adaptive zones of *D. moniliforme* and *D. nobile* will remain relatively stable in the 2050s. In the 2070s, the area of the adaptive zone of *D. moniliforme* will shrink (by up to 16%), while the area of the adaptive zone of *D. nobile* is expected to expand by 1 to 10%, suggesting that *D. nobile* has better adaptability to climate change than *D. moniliforme*.

In recent years, the intensification of conversion of farmland to forest and urbanization has seriously damaged the environment of *Dendrobium*, many species have become extremely rare, and some endemic species with narrow habitat and small geographical distribution are close to extinction. *Dendrobium* species have medicinal and edible value. Relevant research shows that wild *Dendrobium* has greater medicinal activities than greenhouse cultivated *Dendrobium*. Considering the impact of predicted climate change on *Dendrobium* plants, we should carefully investigate the growth characteristics and cultivation methods of each plant, and consider the development of sustainable cultivation methods for the cultivation of the most valuable plants.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

XT and YY: conception and design of the research. XT: acquisition of data and statistical analysis. YY: analysis and interpretation of data. YY and JZ: drafting the manuscript. All authors read and approved the final manuscript.

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