

GEOSPATIAL DISTRIBUTION VARIATION OF THE *PARIS POLYPHYLLA* (MELANTHIACEAE) IN CHINA UNDER CLIMATE CHANGE SCENARIO

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Abstract

Potential geospatial distribution of species supplies momentous information for species management, especially for some plants with high ecological and economic value. *Paris polyphylla* Smith is a medicinal plant with analgesic, hemostatic, anti-inflammatory and anti-tumor activities. Herein, its potential geospatial distribution was calculated under climate change conditions based on 299 known coordinates and 8 environmental layers selected responsible for affecting species distribution. These performances are highly accurate in simulating its geospatial distribution regions, with the AUCs of greater than or near to 0.9 for model building and testing. The key factors were the mean temperature of the coldest quarter (bio11) >7.0°C, the most suitable point is 15°C, the annual mean temperature (bio01) >16.25°C, the temperature seasonality (bio04) from 0 to 650 and the annual precipitation (bio12) >1400 mm. The suitable geographic distribution mostly is located in southwest China, south China, central China, east China and northwest China including increased suitable area, namely, Nyingchi in Tibet with a remarkable reduction to the period of 2050s or 2070s, indicating that the suitable area of the species has a continuous decreasing trend. However, between 2050s and 2070s, the suitable area of the specie is almost unchanged for same greenhouse gas emission scenarios. More importantly, four newly discovered distribution areas including western China (middle-south Shaanxi and southeast Gansu), central China (central and western Hunan), southwest China (Main urban area of Chongqing) and east China (eastern and western Zhejiang), were discriminated as lost suitable areas. Consequently, we should strictly monitor these four newly discovered-lost suitable areas in the future.

Key words: *Paris polyphylla*; Maxent model; Climate change; Potential geospatial distribution.

Introduction

Plant growth and distribution is closely associated to environmental variables including topographical and climatic factors etc., (Jia *et al.*, 2017; Qin *et al.*, 2017). At present, studying the relationship between species and environment variables, finding out the most environmental variables affecting their geospatial distribution, and analyzing the changes of suitable areas under climate change conditions, have become among the research questions in ecology, global change biology and biogeography (Hu *et al.*, 2015; Chen *et al.*, 2022). Among environmental variables, climate (temperature and wetness) is among the most critical factors restricting the geospatial distribution of species, and changes in the distribution pattern of species can most directly and indirectly reflect climate change (Cao *et al.*, 2019; Ran *et al.*, 2019). Global warming will directly affect the plants on the earth and all life forms related to them, and degeneration and fragmentation of native plants are the primary factors of plant endangerment (Li., 2014). According to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), the global climate will become significantly warming, so the precipitation pattern will also change significantly (Hu *et al.*, 2015). As a result, climate change may bring about changes in the geospatial distribution pattern of species, aggravate the reduction of biodiversity and cause the loss of germplasm resources, and even accelerate the extinction of species (Bellard *et al.*, 2012). Therefore, for species protection and sustainable utilization of resources, it is crucial for us to carry out research on the geospatial distribution and its dynamic change of species under climate change conditions.

Fortunately, the species distribution models (SDMs) are the worthwhile tools available free to evaluate species-

surrounding relationship and determine the potential distributing regions for the species, thus have been extensively utilized in ecology and biogeography studies etc. (Guisan & Thuiller, 2005; Wang *et al.*, 2017). However, out of various SDMs, Maximum entropy model (Maxent) has been confirmed to be better and outperformed other SDMs (Phillips *et al.*, 2006; Qin *et al.*, 2017). This model attracting more and more attention of researchers shows lots of merits: (1) to use categorical and continuous data and eliminates interactivity among different variables (Phillips *et al.*, 2006; Wang *et al.*, 2010); (2) only to require occurrence-only data together with some environment variables to attain correctly prediction results; (3) to need lower configuration for computer and always maintain stable and reliable prediction results; (4) to evaluate the weight of each environmental variables by a jackknife command. Therefore, this model is very popular for accurately calculating the geospatial distribution of species and estimating quantitatively species-environment relationships (Wang *et al.*, 2010; Hu *et al.*, 2015; Qin *et al.*, 2017).

The *Paris polyphylla* Smith, belonging to genus *Paris* in the family Liliaceae, is an endangered and rare traditional Chinese herb with analgesic, hemostatic, anti-inflammatory and anti-tumor activities (Jiang *et al.*, 2011). At present, its rhizome is commonly used for the main raw material of more than 260 kinds of Chinese patent medicines such as Yunnan Baiyao, Jidesheng Snake Tablets and so on (Tao *et al.*, 2020). In China, in recent years, due to the serious deterioration of the ecological environment and excessive human excavation, the number of its wild resources have decreased dramatically and its population is distributed in fragments, so that it has become endangered and be classified as plant of the second-class protection (Lu *et al.*, 2013). Meanwhile, to meet the growing needs for this

traditional Chinese herb and relieve the pressure of medical demand, its planting area has gradually begun to appear in southern China, such as Fujian, Jiangxi and Zhejiang (Su *et al.*, 2020), however, this blind introduction and improper cultivation often occur, which seriously restricted the development of the planting industry of the species owing to lack of adaptability analysis of the species. Furthermore, climate change is projected to change species' geospatial distributions and aggravate the loss of forest biodiversity in ecosystems (Li & Chen, 2014; Hu *et al.*, 2015; Qin *et al.*, 2017). Therefore, to avoid investment hazard led to by blindly broadening its potential cultivation regions, it is very urgent for us to evaluate its potential geospatial cultivation regions under climate change conditions. The aims are: (1) to determine the potential cultivation areas of the species in the current condition and identify the most key variables responsible for the potential geospatial distributions; (2) to delineate trends of the species' cultivation regions accompanying with climate change, which will be helpful to the government department for implementing regional planning of the species in China.

Material and Methods

Species distribution samples: A total of 3243 presence points for the *Paris polyphylla* were collected from two free databases, namely, Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/zh/>) and National Specimen Information Infrastructure (NSII) (<http://nsii.org.cn/2017/>). Moreover, some other presence points for this species were mainly gathered from scientific literature published (Su *et al.*, 2020; Zhang *et al.*, 2016, 2017; Lu *et al.*, 2013). In order to enhance the reliability of prediction, the points of introduced and cultivated species and some data that we cannot obtain accurate geographical location were eliminated. The geographic coordinates of presence points were obtained based on the Geo Names geographical data base (<http://www.geonames.org/>). Meanwhile, due to big spatial autocorrelation existing among the observed data of the same distribution area, such presence data may bring about overfitting of the experimental data (Jaryan *et al.*, 2013), so duplicates points were removed too and thus one presence point in each grid (30 m×30 m) was only retained. Finally, 299 presence points in total were ultimately retained and then the coordinates of these points were kept in csv pattern.

Environmental data: The geospatial distribution region of the *Paris polyphylla* is determined by all environmental variables, such as topographical and climatic factors etc., (Wang *et al.*, 2010). Among them, in the current (i.e., in the period of 1950-2000) condition, 19 bioclimatic variables with a 30s (ca. 1km² at ground level) spatial resolution free from the worldclim database (<http://www.worldclim.org>), were used to reflect a combination of annual changes, seasonal characteristic, and extreme environmental conditions (Hijmans *et al.*, 2005; Xu *et al.*, 2014), which are considered biologically more meaningful than only annual or monthly averages of climatic variables (Kumar & Stohlgren, 2009). These World Clim dataset was produced through an

interpolation technique by using monthly records on temperature or precipitation from the years of 1950 to 2000 (Kumar *et al.*, 2014). Meanwhile, through certain calculation formula, we can distinguish the most key variables mainly restricting with the distribution region of the species. Besides, the RCPs (Representative concentration pathways) from the Fifth IPCC Assessment Report (AR5) were declared by IPCC (Intergovernmental Panel on Climate Change) on September 30, 2013 (Hu *et al.*, 2015). Four RCPs (i.e., RCP2.6, RCP4.5, RCP6.0 and RCP8.5) from the worldclim database (http://www.worldclim.com/cmip_5_30s), were coded in the light of a possible range of radiative forcing values in the year of 2100 (+2.6, +4.5, +6.0, and +8.5W•m⁻², respectively), reflecting scenarios in which the radiative forcing values had reached 2.6, 4.5, 6.0 and 8.5 W•m⁻² in the year 2100 (Hu *et al.*, 2015; Yi *et al.*, 2016). Owing to be near to the real climate change by the combination of climate, carbon cycle and socio-economic scenarios (Zhang *et al.*, 2016; Wang *et al.*, 2017), so in this study the potential geospatial distribution region for the species were simulated based on 20 environmental variables including 19 future bioclimatic variables from one global climate models (CCSM4) widely used in some researches (Zhang *et al.*, 2018; Chen *et al.*, 2022) for two periods, 2050s (average for the year of 2041–2060) and 2070s (average for the year of 2061–2080) in two greenhouse gas emission scenarios (RCP4.5 and RCP6.0) and one topographical factor (altitude). The altitude layer was obtained from DEM (i.e., Digital Elevation Model) also downloaded from the above World Clim database. In addition, this altitude layer was unchanged for the model building under climate change conditions. Moreover, the base map (China 1: 4000,000) was acquired from the national fundamental geographic information system (<http://infgis.nsd.gov.cn/>).

Data filtering and modeling procedure: All 20 environmental variables in the study area were extracted by the border map of China based on the above-mentioned raster data. Then, we collected values from all 20 environmental variables combined with 299 presence points. To reduce the influence of multi-collinearity among 20 environmental variables, these extracted values were analysed based on Pearson correlation coefficient in SPSS 19.0. According to the correlation coefficient ($r \geq 0.8$) and taking into consideration the weight of each environmental variables devoted to predictor contributions, the remaining 8 variables were eventually utilized for modelling (Table 1). Meanwhile, to meet the needs of this model, these variables were converted to asc formats. Based on 299 known presence points and 8 environment variables corresponding to presence points of this species, its potential geospatial growing areas were simulated under climate change conditions by this Maxent, a machine learning program based on maximum entropy principle (version 3.4.1; <http://www.cs.princeton.edu/~schapire/maxent/>), mainly because the performances from this model invariably exceed those of other models, so this model is thought as the best-performing tools in evaluating the potential geospatial distribution region for this species (Qin *et al.*, 2017; Wang *et al.*, 2017).

Table 1. The AUC generated in the different periods.

GCMs	Periods	AUC of model building	AUC of Model testing	AUC of Random model
	1950-2000 (Current)	0.9231	0.9005	0.5
CCSM4-rcp4.5	2041-2060 (2050s)	0.9299	0.8805	0.5
	2061-2080 (2070s)	0.9333	0.8880	0.5
CCSM4-rcp6.0	2041-2060 (2050s)	0.9318	0.8860	0.5
	2061-2080 (2070s)	0.9297	0.8835	0.5

During modeling process, 75% of the presence points was randomly utilized for modeling, the remaining for testing (Wang *et al.*, 2010; Qin *et al.*, 2017). Moreover, “jackknife” and “response curves” were ticked. Furthermore, the regularization multiplier value was selected as 0.1 to refrain from the overfitting of the experimental data (Yang *et al.*, 2013). In addition, to ensure the steadiness of prediction results, the model with other default parameter settings was run 10 replicates by cross-validation, and the average value of habitat suitability was considered as the final result in logistic format and asc types (Khanum *et al.*, 2013; Zhang *et al.*, 2022). As a result of the demand of binary maps, the Maximum Youden Index (Maximum training sensitivity plus specificity Logistic threshold) in the current condition was selected as a threshold value (greater (suitable) or less than (unsuitable)), so the continuous maps were converted into suitable regions and unsuitable ones based on the above threshold value (Liu *et al.*, 2013; Xia *et al.*, 2019). The Maximum Youden Index was usually utilized to be the cutoff point, which is superior to other threshold value in transforming the continuous area into ‘suitable area’ and ‘unsuitable one’ (Jimenez-Valverde and Lobo, 2007; Liu *et al.*, 2013). Afterwards, in order to visually see the dynamic difference, we multiply the current result by the future predicted ones and then identified the expanding and shrinking suitable areas of this species.

Model performance and influencing factors: The AUC (Area under the receiver curve) was widely utilized to evaluate the percent of accuracy from modeling in much research (Wang *et al.*, 2010; Hu *et al.*, 2015). The AUC varied from 0.5 to 1.0. Specifically, AUC=0.5 shows that modeling does not exceed random, whereas AUC=1.0 shows a best model, but performance is excellent when the value of AUC is near or more than 0.9 (Kumar *et al.*, 2014; Hu *et al.*, 2015). Based on the jackknife method, permutation importance and percent contributions, we could distinguish the dominant factors relative to other variables for the species’s habitat suitability (Xiong *et al.*, 2019; Zhang *et al.*, 2022). Besides, response curves produced automatically by this Maxent model were applied to analyse the quantitative species-surrounding relationship (Hu *et al.*, 2015).

Result

Modeling evaluation and current geographic distribution:

The value of AUC was widely utilized to assess the accuracy of model building in many ecological researches. In this present study, the AUCs of modeling and testing are more than 0.9 for the prediction performances under the current conditions (Table 1). It was indicated that the prediction performance is excellent for prediction of this species. Based on the Maximum Youden Index (the average value of 0.2343 in 10 replicates) as a cutoff point under the current condition (Table 1), the final distribution map was reclassified into the suitable area and unsuitable one. The suitable region of the *Paris polyphylla*, in the study region mainly is concentrated

on five areas including southwest China (Yunnan, Guizhou, Chongqing, eastern and southern Sichuan and newly identified area, namely, Nyingchi in Tibet), central China (most of Hunan, the entire Jiangxi and western Hubei), south China (Guangxi, Guangdong and Hainan), east China (Fujian, Zhejiang and Taiwan) and northwest China (middle-south Shaanxi and southeast Gansu). As indicated in (Fig. 1), the range of the suitable areas for the *P. polyphylla* is roughly similar to the actual distribution obtained by our collected data, so the above-mentioned threshold value is applicable. The analysis after projection (Asia North Albers Equal Area Conic) showed that the suitable and unsuitable areas accounted for 20.94% and 79.06% in the whole study region, respectively.

Environmental variable assessment and their threshold:

Permutation importance is the value of individual environmental variable on the training occurrence and background points. And the bigger the value is, the larger the dependence of the model is on this variable (Zhang *et al.*, 2020). Of 8 environmental variables, based on permutation importance, the temperature seasonality (bio04) with 30.2%, had the highest score (Table 2), indicating that this variable significantly has an effect on the distribution of the *Paris polyphylla* under the current condition; and then followed by the annual mean temperature (bio01) and annual precipitation (bio12), with 23.7% and 22.3% respectively. The cumulative permutation importance of these three parameters amounted to 76.2%. Meanwhile, the percent contributions of the mean temperature of the coldest quarter (bio11) were 67.9% and then followed with the temperature seasonality (bio04) with 16.0% (Table 2), so the sum of them amounted to 83.9%, implying that these top two variables have a strong influence on the current geospatial distribution of *P. polyphylla*. In general, the key bioclimatic variables responsible for affecting the geospatial distribution of the *P. polyphylla* are the mean temperature of the coldest quarter (bio11), the annual mean temperature (bio01), the temperature seasonality (bio04), and the annual precipitation (bio12). In addition, based on the jackknife test, the mean temperature of the coldest quarter (bio11) and the annual precipitation (bio12) significantly affected the geospatial distribution of the *P. polyphylla* (Fig. 2). Taken together, four dominant environmental variables were the mean temperature of the coldest quarter (bio11), the annual mean temperature (bio01), the temperature seasonality (bio04) and the annual precipitation (bio12). To further clarify the above-mentioned four key factors’ impacts on the distribution of *P. polyphylla*, the response curves were produced automatically with four variables alone. It is shown that the thresholds for the above-mentioned four key variables (Probability of existence >0.5) were: the mean temperature of the coldest quarter (bio11) ranged from >7.0°C, the most suitable point is 15°C; the temperature seasonality (bio04) from 0 to 650; the annual precipitation (bio12) > 1400 mm; the annual mean temperature (bio01) >16.25°C (figures are not shown).

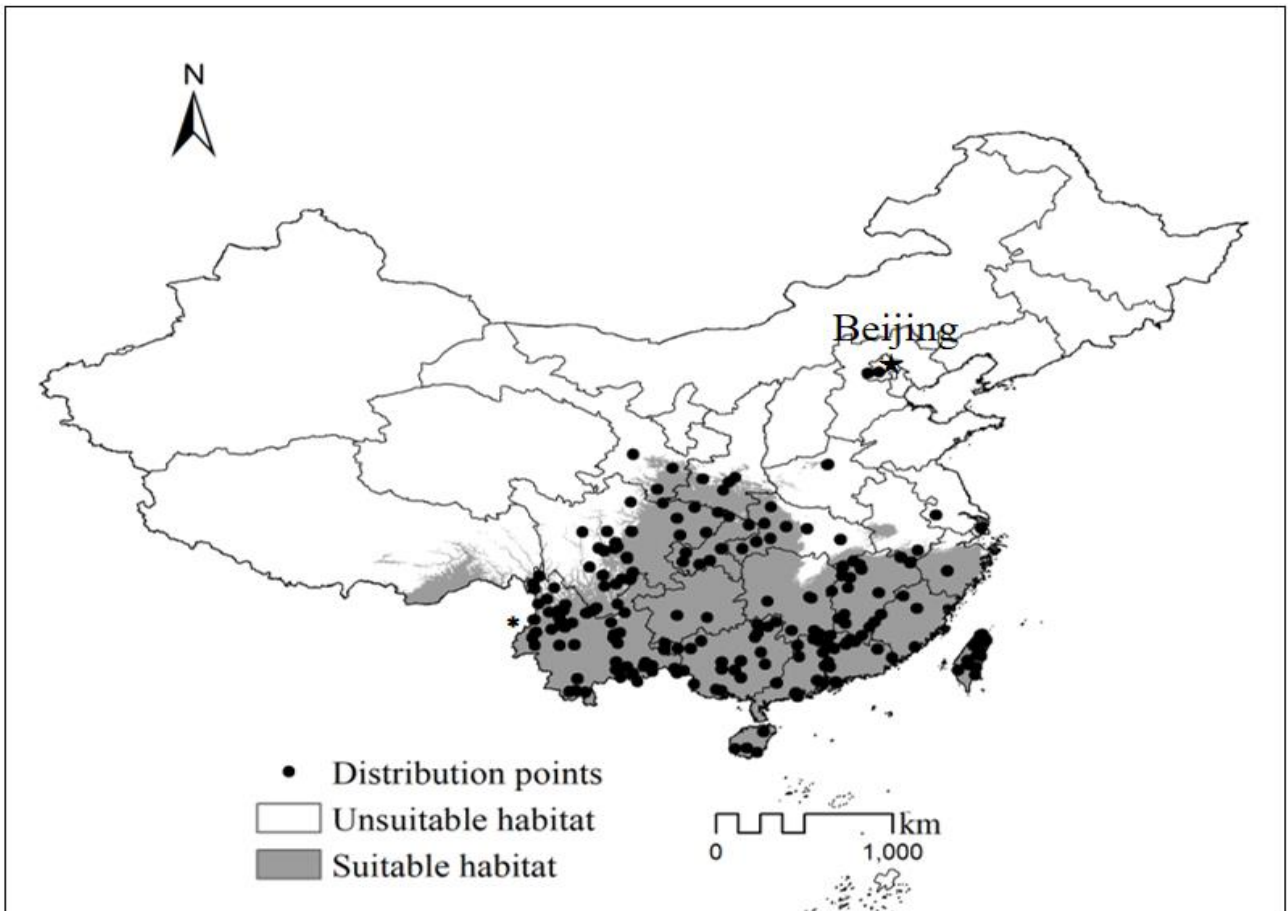


Fig. 1. The potential geospatial distribution of *P. polyphylla* in the periods of 1950-2000.

Jackknife of Rrgularized training gain for *Paris Polyphylla_3*

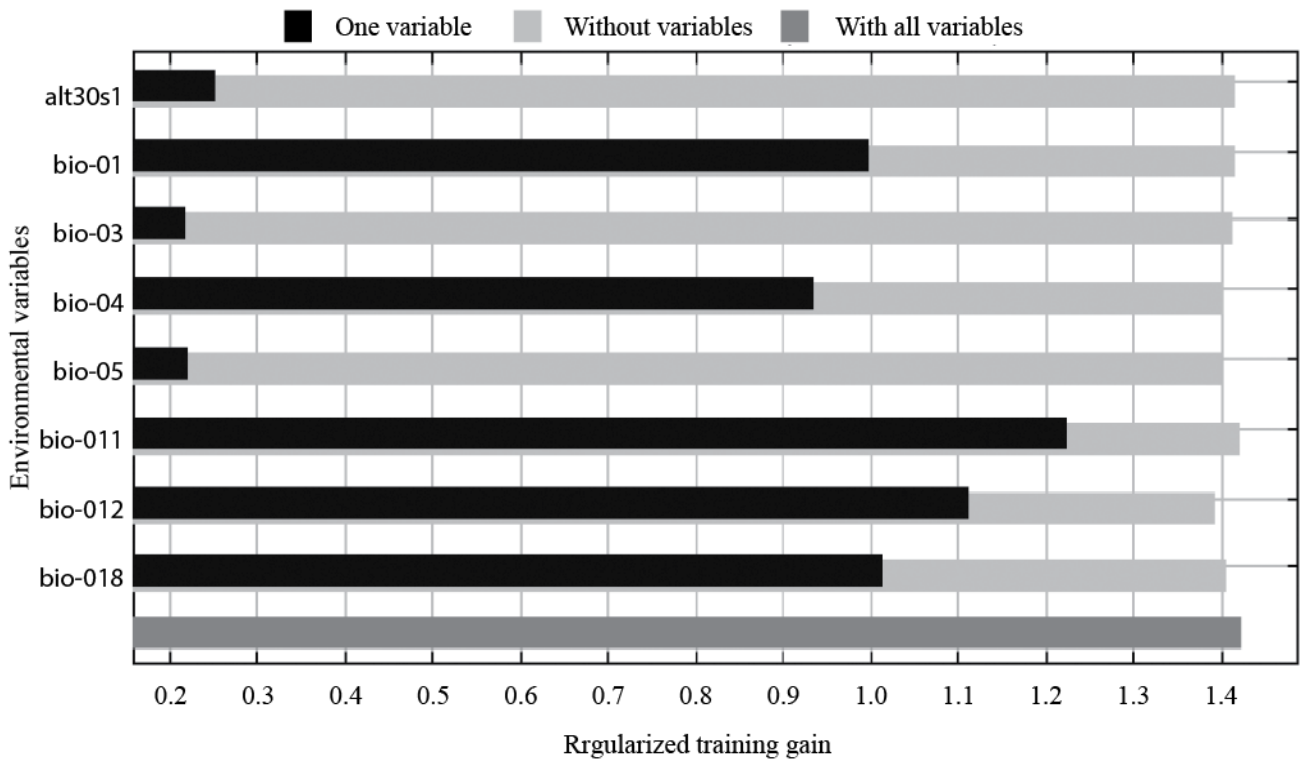


Fig. 2. Jackknife test for assessing the weight of each environmental variables on the geospatial distribution of *P. polyphylla* under the current condition.

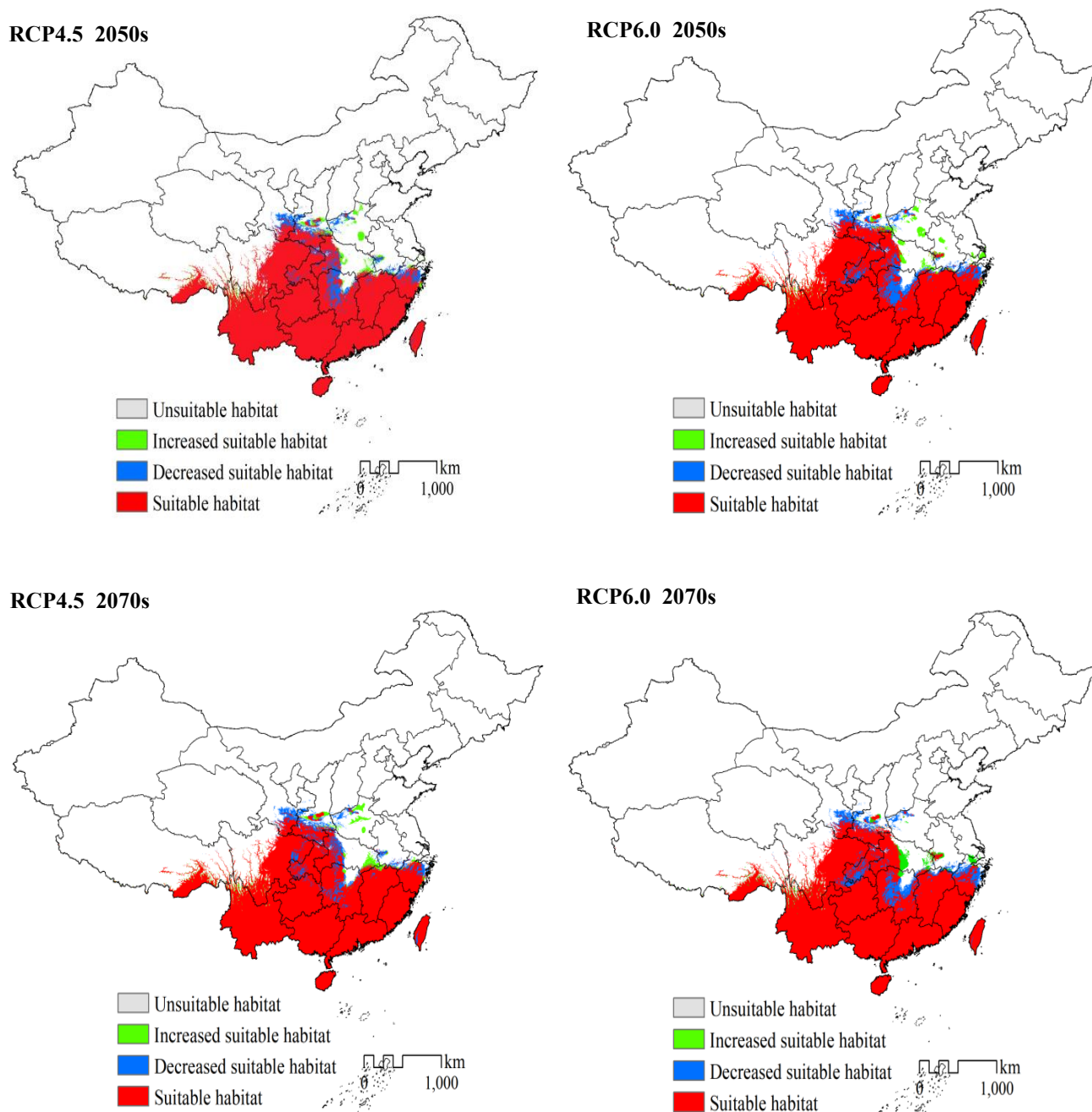


Fig. 3. Geospatial distribution of suitable habitat for the *P. polyphylla* in different periods.

Changes in the geospatial distribution of *P. polyphylla*:

This model is also used to simulate its geographic distribution trends from the period of 2050s to 2070s. Therein, these performances in the future environmental conditions were excellent, with an AUC of near to or greater than 0.9 for modeling and testing. According to the same cutoff point from the maximum Youden under the current condition, habitat suitability for the *Paris polyphylla* is reclassified into a binary suitable/unsuitable map, and their areas are computed based on the same projection coordinate systems. As shows in (Fig. 1 and 3), under climate change conditions, these results indicate similar spatial pattern in the suitable areas of *P. polyphylla*, however, compared with ones under the current condition, its suitable areas show spatial pattern of expansion and shrinking. Taken altogether, the suitable areas of *P.*

polyphylla in the study area show an lost trend only because these lost regions are bigger than the increased ones (Table 3 and Fig. 3). however, between 2050s and 2070s, the suitable area of the specie is almost unchanged for same greenhouse gas emission scenarios. More importantly, in the period of 2050s and 2070s, four discovered suitable distribution areas including western China (central Shaanxi and eastern Gansu), central China (central Hunan and western Hunan), southwest China (Main urban area of Chongqing) and east China (eastern and northern Zhejiang), were identified as reduced suitable areas by the Maxent model, indicating that these suitable habitats in China are going to downgrade the development and utilization for the *P. polyphylla*. Consequently, we should strictly monitor these four newly discovered-lost suitable areas in the future (Fig. 2).

Table 2. The percent contribution and permutation importance of eight environmental variables under the current condition.

Code	Description	Percent contribution	Permutation importance	Code	Description	Percent contribution	Permutation importance
bio11	Mean temperature of the coldest quarter	67.9	6.0	bio18	Precipitation of warmest quarter	2.6	4.0
bio04	Temperature seasonality	16.0	30.2	bio03	Isothermality	1.9	3.2
bio01	Annual mean temperature	4.7	23.7	bio05	Maximum temperature of the warmest month	1.7	5.6
bio12	Annual precipitation	4.2	22.3	alt30s1	Altitude	1.1	5.0

The highlighted variables, selected through their contribution and permutation importance, were four main influencing factors

Table 3. Increased and lost areas of suitable potential distribution for the *P. polyphylla* under future environmental conditions from CCSM4 global climate model.

Comparative periods	Climate scenario	Increased habitat		Lost habitat		Total change	
		Suitable /km ²	Percentage %	Suitable/ km ²	Percentage %	Suitable/ km ²	Percentage %
Current-2050s	RCP4.5	80725.1	3.11	189195	7.28	108469.5	4.18% (-)
	RCP6.0	91215.5	3.51	230241	8.86	139025.5	5.35% (-)
Current-2070s	RCP4.5	84144.8	3.24	193859	7.46	109714.2	4.22% (-)
	RCP6.0	76691.3	2.95	231849	8.93	155157.7	5.97% (-)

Note: the suitable areas under the current condition (1950-2000 year) are 2,597,430 km²

Discussion

The *Paris polyphylla* (Smith) is a traditional Chinese medicine in China attracting more and more attention of researchers throughout the world with the analgesic, hemostatic, anti-inflammatory and anti-tumor activities (Jiang *et al.*, 2017). In China, it presently grows under forests with an altitude of 1800 m to 3200 m in Guizhou, Yunnan, Tibet, Sichuan, Guangxi, Hunan, Taiwan of China etc. (Zhang *et al.*, 2017). In recent years, the medicinal materials rely on mining wild resources accompanied by the increasing demand and rising price, so the actual distribution areas of this population have been gradually reduced and be in fragments (Lu *et al.*, 2013). To meet the increasing demand for the *P. polyphylla*, the southern region including Fujian, Jiangxi and Zhejiang etc. in China has tried to plant this species (Su *et al.*, 2020). However, nowadays, very little is aware of the potential geospatial areas of *P. polyphylla*, thus posing great challenges for relevant managers to expand the planting area. Fortunately, nowadays, species distribution modeling (SDMs) has been become prominent tools for predicting the potential geospatial distribution of a species (Wang *et al.*, 2010; Qin *et al.*, 2017). Among SDMs, the Maxent model can consistently performs better with presence-only data compared with other models and be widely utilized for estimating the geospatial distribution of suitable area for species in many field (Khanum *et al.*, 2013; Wang *et al.*, 2017). In this study, these accuracies from this model are very excellent, with AUCs of near to or greater than 0.9 for modeling and testing under climate change conditions. In addition, based on above-mentioned predicting outcomes (Fig. 1), the suitable area was highly in line with the actual geospatial distribution of the *P. polyphylla*, indicating that the results from this model were accurate and the threshold value under the current condition was reliable. As shown in Fig. 1, besides the actual distribution of the species, a

newly identified area, namely, Nyingchi in Tibet was predicated as the suitable area, indicating that the actual geospatial distribution area of the species was very smaller than ones that the model simulated, and Nyingchi in Tibet can be used as a new development zone. In addition, the above-mentioned predicting outcomes indicate that these suitable growing regions of the species in future conditions will be similar as one in current condition, i.e., these suitable regions will be mostly located in southwest China, central China, south China and east China and northwest China. In 2050s and 2070s (Table3), the suitable planting regions were simulated to reduce bit by bit by 108469.5~139025.5 km² and 109714.2~155157.7km² separately, further indicating that between the period of 2050s and 2070s, the suitable area is almost unchanged for same greenhouse gas emission scenarios (RCP4.5. or RCP6.0). To periods of 2050s and 2070s, four discovered suitable distribution areas including western China (middle-south Shaanxi and southeast Gansu), central China (central Hunan and western Hunan), southwest China (Main urban area of Chongqing) and east China (eastern and northern Zhejiang), were identified as lost suitable areas compared with ones under current condition, so it is very important for us to strictly monitor these four newly discovered-lost suitable areas hereafter (Fig. 2).

The geospatial distribution area of species was mostly affected by temperature, rainfall, terrain and so on (Lei & Chen, 2014; Jia *et al.*, 2017). Out of them, climate is among the most notable factors responsible for the geospatial distribution of species on the earth (Gao *et al.*, 2018). Some researchers have shown that the main factors affecting the geospatial distribution of botany is the cold endurance of botany (Woodward, 1987; Hu *et al.*, 2015), which is consistent with our recent findings that the contributions of the mean temperature of the coldest quarter (bio11) were 67.9%, with thresholds of > 7.0°C, the most suitable point is 15°C. According to the recent laboratory studies, in the wet

sand substrate test, it was found that the seed dormants for 240 days and continues to culture at 18°C, the radicle of its seed develops into a taproot (Huang *et al.*, 2016), being basically identical to our research results. The temperature seasonality (bio04) and the annual precipitation (bio12) with thresholds of 0 to 650 and > 1400 mm respectively indicated that it is suitable for living in the habitat with relatively humid climate, which is consistent with previous studies that it tends to be the shade and afraid of the strong light under the forest with humid climate and appropriate rainfall (Li., 2014). In general, the suitable temperature for seed germination, root growth and development, and tip bud germination is 18~20°C (Li., 2014), which matched basically with the annual mean temperature (bio01) from >16.25°C.

It is generally believed that four factors determining the distribution area of species are: environmental factors, biological factors, species' diffusion ability, and species' adaptation to the new environment (Soberon & Peterson, 2005; Ju *et al.*, 2010; Jia *et al.*, 2017). However, our paper only considers some of the environmental factors as prediction indicators, which is still a certain gap with the actual situation and needs further research.

Conclusions

(1) The suitable area of the *Paris polyphylla* in China mostly is located in southwest China, central China, south China and east China and northwest China including increased suitable area, namely, Nyingchi in Tibet. (2) The key factors were the mean temperature of the coldest quarter (bio11) > 7.0°C, the most suitable point is 15°C, the annual mean temperature (bio01) >16.25°C, the temperature seasonality (bio04) from 0 to 650 and the annual precipitation (bio12) > 1400 mm; (3) Under climate change conditions, the suitable area of the species has a continuous decreasing trend. however, the suitable area of the specie is almost unchanged for same greenhouse gas emission scenarios between 2050s and 2070s, Furthermore, four newly discovered distribution areas including western China (middle-south Shaanxi and southeast Gansu), central China (central Hunan and western Hunan), southwest China (Main urban area of Chongqing) and east China (eastern and northern Zhejiang), were distinguished as lost suitable regions.

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