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Abstract: Pinus densiflora is an important evergreen coniferous species with both economic and ecological value. It is an endemic species in East Asia. Global climate warming greatly interferes with species survival. This study explored the impact of climate change on the distribution of this species and the relationship between its geographical distribution and climate demand, so as to provide a theoretical basis for the protection of *P. densiflora* under the background of global warming. This research used 565 valid data points and 19 typical climatic environmental factors distributed in China, Japan, and South Korea. The potential distribution area of P. densiflora in East Asia under the last glacial maximum (LGM), mid-Holocene, the current situation and two scenarios (RCP 2.6 and RCP 8.5) in the future (2050s and 2070s) was simulated by the MaxEnt model. The species distribution model toolbox in ArcGIS software was used to analyze the potential distribution range and change of P. densiflora. The contribution rates, jackknife test and environmental variable response curves were used to assess the importance of key climate factors. The area under the receiveroperating characteristic curve (AUC) was used to evaluate model accuracy. The MaxEnt model had an excellent simulation effect (AUC = 0.982). The forecast showed that the Korean Peninsula and Japan were highly suitable areas for P. densiflora, and the area had little change. Moreover, during the LGM, there was no large-scale retreat to the south, and it was likely to survive in situ in mountain shelters. The results suggested that Japan may be the origin of *P. densiflora* rather than the Shandong Peninsula of China. The distribution area of P. densiflora in the mid-Holocene and future scenarios was reduced compared with the current distribution, and the reduction of future distribution was greater, indicating that climate warming will have certain negative impacts on the distribution of P. densiflora in the future. The precipitation of the warmest quarter (Bio18), temperature seasonality (Bio4), mean annual temperature (Bio1) and mean temperature of the wettest quarter (Bio8) had the greatest impact on the distribution area of P. densiflora.

Keywords: Pinus densiflora; climate change; habitat distribution; MaxEnt

1. Introduction

Since the Quaternary Period (from 2.58 Ma to now), the drastic changes in the earth's climate had an important impact on the current distribution pattern of species [1]. According to the sporopollen data, under the background of global cooling during the last glacial maximum (LGM), the vegetation types in Eurasia and North America retreated to the equator, and the forest area decreased and fragmented to varying degrees [2]. In the recent warm period (mid-Holocene), due to the high temperature and humidity, the forest belt in the northern middle latitude of Eurasia moved slightly northward, and the warm temperate evergreen broad-leaved forest and mixed forest in China also moved northward [2,3]. Obviously, climate has far-reaching impacts on the distribution range of species and is a key factor determining the distribution of species on a large scale [4].

The fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC) points out that the global climate is obviously warming [5]. With global warming, species



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). distribution, population size and genetic diversity will change [6], which will lead to plant migration, endangerment and even extinction [7–12]. Therefore, we should study the response of the plant distribution pattern to climate change and understand the climate demand of organisms and its relationship with the species geographical distribution. It is important to reveal the history of species formation, migration and diffusion and to put forward reasonable strategies for species diversity protection [13].

Species distribution models have been widely used to study the effects of climate change on the potential geographic species distribution based on maximum temperature, minimum temperature, relative humidity, rainfall and other environmental factors [14–19]. The MaxEnt model can simulate the potential geographic distribution of species based on environmental variable layers, species distribution records, machine learning and the maximum entropy principle. The MaxEnt model is suitable where the number of species distribution points is uncertain and the correlation between environmental variables is unclear [20,21]. Therefore, it is very suitable for modeling species distribution [22–24]. Moreover, MaxEnt is suitable when compared with other current approaches because it works with "presence data only" and cannot detect and collect 'absence data', which are rarely available [18,25]. The MaxEnt model has a continuous output (a maximum likelihood estimate of the relative probability of presence) instead of a deterministic role [26]. The MaxEnt model is widely used to study the relationship between species distribution dynamics and climate change [27]. It is also used to predict the sanctuary of organisms during the ice age [28,29].

P. densiflora can endure drought and barrenness, is an excellent pioneer species for secondary succession, and, thus, is crucial for reforestation and soil and water conservation [30]. The seed propagation of *P. densiflora* can be used for reforestation in the steeper barren hills. It can also be used as an ornamental tree species for afforestation in the sandy land on both sides of rivers [31]. *P. densiflora* is one of the established species of temperate coniferous forests in temperate and warm temperate forest regions. Moreover, a large area of forest communities has formed in the eastern part of the Liaodong Peninsula and Jilin Province, South Korea, North Korea, Russian Far East, and Japan [32]. Therefore, *P. densiflora* is endemic to East Asia. However, global warming may change the distribution of the *P. densiflora* due to the associated climate factors.

Many studies have assessed the population ecology, community characteristics, management techniques, and individual growth characteristics of *P. densiflora* in China and abroad [33,34]. However, no study has reported on the suitable distribution of *P. densiflora*. This study developed a prediction model employing extensive geo-referenced collections, field surveys data, presence data, and bioclimatic variables via a species distribution model with MaxEnt software. This study aimed to: (1) identify the most significant environmental factors influencing the potential distribution of *P. densiflora* and (2) predict the change trend of the geographical distribution of *P. densiflora* in different historical periods so as to provide a scientific basis for the formulation of protection policy, the delimitation of reserve and resource management of *P. densiflora*.

2. Materials and Methods

2.1. Data Collection

This study collected the distribution data of *P. densiflora* from the Global Biodiversity Information Facility (https://www.gbif.org (accessed on 25 November 2021)), the Chinese Virtual Herbarium (http://v5.cvh.org.c/ (accessed on 25 November 2021)), and survey data. The data were sifted to eliminate repetitive samples and any samples without detailed location information. Duplicate records were deleted and filtered spatially so that only one point occurred within each grid cell (10 km × 10 km). This study obtained 565 comprehensive and accurate distribution records (Figure 1). The longitude and latitude coordinates of the samples were recorded in the Excel database and converted into CSV format for developing the MaxEnt model.



Figure 1. Current distribution sites and potential distribution area of *P. densiflora*.

2.2. Climatic Data

Environmental variables are key factors affecting species distribution. The climate data of the LGM, the mid-Holocene and the current climate data include 19 bioclimatic variables. This study selected the 19 bioclimatic variables (Bio1-Bio19) from the world climate database (www.worldclim.org (accessed on 20 May 2021)) using a spatial resolution of 2.5 arc-minutes [35]. The future climate data (2050s and 2070s) were determined based on the CCSM4 model, which has a strong simulation capability [36]. The model has four emission scenarios from the Fifth Emission Report of the IPCC. This study chose the lowest and the highest emission scenarios, RCP2.6 and RCP8.5, respectively. The ArcGIS conversion tool was used to convert the environmental factors into the ASCII format.

2.3. Model Simulation

MaxEnt software (MaxEnt 3.3.3 http://www.cs.princeton.edu/wschapire/Maxent/ (accessed on 10 May 2020)) was used for modeling [37]. This study used 75% of the data for training, and the remaining 25% were used to test the model's ability to predict the species distribution. Threshold-independent receiver-operating characteristic analysis (ROC) was used to calibrate the model and validate its robustness. The area under the receiver-operating characteristic curve (AUC) was used for additional precision. A jackknife test was used to assess the relative importance of each variable [17]. Through SPSS 23.0 software, the Pearson correlation coefficient was used to test the multicollinearity among the 19 climatic variables, and, finally, 7 climatic variables were selected for subsequent modeling [38] (Table 1). ArcGIS 10.4 software was used for visual processing, and a natural breakpoint classification method was adopted. According to the corresponding fitness index (FI), the distribution area of *P. densiflora* was divided into four grades: high suitability (FI \geq 0.6), medium suitability (0.4 \leq FI < 0.6), low suitability (0.2 < FI < 0.4) and not suitable (FI \leq 0.2) [39]. The distribution prediction map of the potential fitness area of *P. densiflora* in East Asia was drawn.

Abbreviation	Description	Whether to Use for Modeling
Bio1	Mean Annual Temperature (°C)	Yes
Bio2	Mean Diurnal Range (Mean of monthly (max temp-min temp)) (°C)	No
Bio3	Isothermally (Bio2/Bio7) (×100)	Yes
Bio4	Temperature Seasonality (standard deviation $\times 100$) (C of V)	Yes
Bio5	Max Temperature of Warmest Month (°C)	No
Bio6	Min Temperature of Coldest Month (°C)	No
Bio7	Temperature Annual Range (Bio5–Bio6) (°C)	No
Bio8	Mean Temperature of Wettest Quarter (°C)	Yes
Bio9	Mean Temperature of Driest Quarter (°C)	Yes
Bio10	Mean Temperature of Warmest Quarter (°C)	No
Bio11	Mean Temperature of Coldest Quarter (°C)	No
Bio12	Annual Precipitation (mm)	No
Bio13	Precipitation of Wettest Month (mm)	Yes
Bio14	Precipitation of Driest Month (mm)	No
Bio15	Precipitation Seasonality (C of V)	No
Bio16	Precipitation of Wettest Quarter (mm)	No
Bio17	Precipitation of Driest Quarter (mm)	No
Bio18	Precipitation of Warmest Quarter (mm)	Yes
Bio19	Precipitation of Coldest Quarter (mm)	No

Table 1. Environmental data used in this study.

2.4. Geospatial Analysis

ArcGIS 10.4 software was used to calculate the area of the different suitable areas in each period, and SDM toolbox 2.4 tool was used to calculate the potential distribution area and distribution center change of *P. densiflora* in the different periods. In ArcGIS 10.4 software, the "reclass" function was used to modify the grid values corresponding to the suitable and not suitable areas that were predicted in each period of *P. densiflora* to 1 and 0, respectively, and then to add the SDM toolbox and select the "MaxEnt Tools" subdirectory in the "SDM Tools" module. The "distribution changes between binary SDMs" tool was used to successively calculate the area change range of the potential distribution areas in each period and to obtain the expansion area, stable area and contraction area of the distribution. The "centroid changes (lines)" tool was used to calculate the geometric center of displacement of the predicted distribution in the different periods and to detect the overall change trend of the *P. densiflora* distribution area [40].

3. Results

3.1. Evaluation of MaxEnt Model Prediction Accuracy

The MaxEnt3.3.3k software was used to simulate the potential geographic distribution of *P. densiflora* in East Asia based on 565 current distribution record data points and 7 climatic variables. The average AUC value of the 10 replicates was 0.982 (Figure 2), indicating an excellent level. The AUC values of the LGM, mid-Holocene and future (2050s and 2070s) simulations were as high as 0.980 or more, indicating that the prediction results of the MaxEnt model were accurate and suitable.

3.2. Climate-Dominant Factors and the Potential Distribution Areas of P. densiflora

The precipitation of the warmest quarter (Bio18) (67.7%), temperature seasonality (Bio4) (13.9%), mean annual temperature (Bio1) (6.6%), mean temperature of the wettest quarter (Bio8) (5.6%) and isothermality (Bio3) (5.1%) had the greatest impacts on the distribution range of the *P. densiflora* population (Figure 3, Table 2). These results show that precipitation and temperature are the main environmental factors affecting the distribution of *P. densiflora* plants in East Asia. The response curve of *P. densiflora* plants to the main climatic factors is shown in Figure 4. When the FI was greater than or equal to 0.6, the suitability grade was a high-suitability distribution. The precipitation of the warmest quarter (650–800 mm), temperature seasonality (900–1050), mean annual temperature



(10–13 $^\circ\text{C})$ and mean temperature of the wettest quarter (23–24 $^\circ\text{C})$ were the major climatic factors at this time.

Figure 2. ROC test of the MaxEnt model.



Figure 3. The impacts of the environmental variables on the distribution gain of *P. densiflora* detected using the jackknife test.

Table 2. Contribution rate of the climatic factors.

Abbreviation	Description	Contribution (%)
Bio1	Mean Annual Temperature (°C)	6.6
Bio3	Isothermality ($Bio2/Bio7$) (×100)	5.1
Bio4	Temperature Seasonality (standard deviation ×100) (C of V)	13.9
Bio8	Mean Temperature of the Wettest Quarter (°C)	5.6
Bio9	Mean Temperature of the Driest Quarter (°C)	0.2
Bio13	Precipitation of the Wettest Month (mm)	0.9
Bio18	Precipitation of the Warmest Quarter (mm)	67.7



Figure 4. Response curves of the major climate factors. (a) Precipitation of the Warmest Quarter (mm), (b) Temperature Seasonality (standard deviation $\times 100$) (C of V), (c) Mean Annual Temperature (°C), (d) Mean Temperature of the Wettest Quarter (°C).

The current distribution area of *P. densiflora* was mainly between 32–45.3° N and 114–141° E (Figure 1). The total suitable area was about 3.62×10^6 Km². The areas of the high-, medium- and low-suitability areas were about 5.24×10^5 Km², 5.81×10^5 Km² and 1.42×10^6 Km², respectively (Table 3). Heilongjiang, Jilin, Liaoning, Shandong, Jiangsu, Zhejiang, Fujian, Jiangxi, Hubei, Hunan, Guizhou, Henan, Hebei, North Korea, Korea and Japan were the suitable areas for *P. densiflora*. The Korean Peninsula, Japan and China's Jilin Province, Liaoning Province and Shandong Province were the highly suitable areas. Zhejiang, Jiangxi and Hubei had some fragmented distribution (Figure 1).

Period	Low Suitability Area/10 ⁴ km ²	Moderate Suitability Area/10 ⁴ km ²	High Suitability Area/10 ⁴ km ²	Total Suitable Area/10 ⁴ km ²
LGM	128.78	59.41	80.6	268.79
Mid-Holocene	171.32	76.27	72.29	319.88
Current	232.75	74.69	54.62	362.06
PCR2.6-2050	142.21	58.18	52.36	252.75
PCR2.6-2070	119.92	49.86	61.27	231.05
PCR 8.5-2050	131.11	58.66	53.79	243.56
PCR 8.5-2070	127.52	46	56	229.52

Table 3. Dynamics of the changes in the suitable habitat area under the different climate scenarios.

3.3. Potential Distribution and Changes of P. densiflora

In the LGM, mid-Holocene, current situation and future scenarios, the suitable area shows a single-peak trend, and the current area is the peak (Figures 1 and 5, Table 3). The total suitable areas of the LGM and the mid-Holocene decreased by 25.76% and 11.65%, respectively. However, the high-suitability area increased by 47.56% and 32.35%, respectively. During the LGM and the mid-Holocene, the medium-suitability area decreased by 20.46% and 20.12%, respectively, and the low-suitability area decreased by 44.67% and 26.40%, respectively. Under the RCP 2.6 scenario, the total suitable area in 2050 will be about 2.52×10^6 km², 30.19% less than the current distribution area. The high-suitability area will decrease by 41.3%, the medium-suitability area will decrease by 22.10% and the

low-suitability area will decrease by 38.90%. The total suitable area in 2070 will be about 2.31×10^6 km², 36.18% less than the current distribution area. The high-suitability area will increase by 12.18%, the medium-suitability area will decrease by 33.24% and the low suitability area will decrease by 48.48%. Under the scenario of RCP 8.5, the total suitable area in 2050 will be about 2.43×10^6 km², 32.73% less than the current distribution area. The high-suitability area will increase by 1.50%, the medium-suitability area will decrease by 21.46% and the low-suitability area will decrease by 43.67%. In 2070, the total suitable area will be about 2.30×10^6 km², 36.61% less than the current distribution area. The high-suitability area will decrease by 2.53%, the medium-suitability area will decrease by 38.41% and the low-suitability area will decrease by 45.21% (Table 3, Figure 5).



Figure 5. Potential distribution of *P. densiflora* in different periods.

As can be seen from Figures 6 and 7, the centroid $(123^{\circ}33' \text{ E}, 36^{\circ}2' \text{ N})$ of the habitat in the LGM period was close to the Shandong Peninsula. Compared with current situation, the latitude was increased by 3.42° , and the distribution area was shrinking in most directions, only slightly expanding in the northwest and northeast. The centroid $(118^{\circ} \text{ E}, 33^{\circ}59' \text{ N})$ of the habitat in the mid-Holocene was in Jiangsu Province, China. Compared with the current, the latitude was increased by 1.36° , and the distribution area has obviously contracted in the southeast and northeast, with slight expansion in the other directions. Under the RCP 2.6 scenario, the distribution center of *P. densiflora* in 2050 will be located in Anhui Province, China, which is about 0.46° higher than the current distribution center latitude. The distribution area will obviously shrink in southeast and northeast China, will slightly expand in northwest and northeast China and new suitable areas will appear in areas close to Russia. The distribution center of *P. densiflora* in 2070 will increase by 0.42° compared with that of 2050. The distribution area will contract significantly in southeast and northeast China, and new suitable areas will appear in the coastal areas of Russia (Figures 6 and 7).

Under the RCP 8.5 scenario, the distribution center in 2050 will also be located in Anhui Province, China, which is about 0.72° higher than the current distribution center. The distribution area will shrink significantly in northeast and southwest China, will only expand slightly in a few areas and new suitable areas will appear in the coastal areas of Russia. The distribution center of *P. densiflora* in 2070 will decrease by 0.1° compared with that of 2050. The distribution area will contract significantly in northeast China, and new suitable areas will appear in the coastal areas of Russia (Figures 6 and 7).



Figure 6. Geographical distribution changes of P. densiflora in different periods.



Figure 7. Migration route of *P. densiflora* in East Asia under different climates.

4. Discussion

A detailed understanding of species distribution is crucial for the rehabilitation and use of a species in an ecosystem [24,41]. This study performed a detailed analysis of the suitable habitat for *P. densiflora*, providing an important first step in developing strategies and policies for the management and utilization of *P. densiflora*.

4.1. Evaluation of the MaxEnt Model

Models are usually evaluated using overall accuracy, sensitivity, specificity, kappa and true skill statistic indicators [42,43]. The threshold cannot affect the ROC curve. As a result, the ROC curve is presently considered one of the best evaluation indicators. MaxEnt software can directly draw the ROC curve and calculate the AUC value of the model and is, thus, convenient for judging the predictive effect of the model. Therefore, ROC curves are widely used in the evaluation of MaxEnt models. The stability of a model is usually verified using 10 repeated AUC values. Herein, the average AUC value of the 10 repeated runs of the model was 0.982, indicating that the simulation effect was 'excellent', and, thus, the model can be used to simulate the potential distribution of *P. densiflora* in East Asia [44].

4.2. Habitat Suitability Response to Environmental Variables

Herein, Bio18, Bio4, Bio1 and Bio8 were the predominant variables influencing the potential distribution of *P. densiflora*, indicating that those factors play important roles in its distribution. Bio18 is one of the environmental factors affecting plant growth and can be used to understand the effect of climate change on plant species diversity [45]. Precipitation is correlated with many environmental factors influencing the physiological and biochemical processes of plants, e.g., soil moisture is the main factor affecting the plant assimilation rate [46]. Excessive water can cause root rot, promoting pest and disease invasion, especially at high temperatures and extremely high humidity [47]. Herein, the optimal Bio18 value of P. densiflora was 650-800 mm, indicating a greater demand for precipitation, consistent with the current distribution of *P. densiflora*. Moreover, the high-suitability area was mainly in the temperate coastal mountains and plains. P. densiflora is a strong light-loving species. Moreover, it has a strong cold resistance and is not affected by frost damage at -40 °C, indicating that *P. densiflora* has strong adaptability to low temperatures. The response curves of Bio4, Bio1 and Bio8 showed that temperature significantly affects P. densiflora. However, the predicted reduction of the suitable area of P. densiflora in the future showed that it is very sensitive to climate change. Therefore, a reasonable cultivation technique must be adopted based on the growth traits when cultivating *P. densiflora* in different regions.

Besides the above climatic factors, some other factors, such as soil texture and human activities, can influence the suitable habitats for *P. densiflora*. Sandy soil is loose and allows water discharge. Poor water discharge can cause plant disease, insect attack and root rot. Therefore, sandy soils can effectively avoid such issues. The effects of land use transformation can also significantly increase the spatial extent of unsuitable habitats [48]. Although this study suggested that *P. densiflora* has a wide distribution area, much of the suitable area may disappear due to human exploitation. Therefore, further studies are needed to verify the anthropogenic effects on the adaptation of *P. densiflora* to future climates.

4.3. Geographical Distribution and Change of P. densiflora

Although fossil sporopollen data show that the cold and dry climate during the Quaternary glacial period forced many plants to migrate and take refuge southward, and the northern boundary of the evergreen broad-leaved forest retreated southward (24° N) [2]. However, a large number of phylogeographic studies have revealed the pattern of in situ refuge of subtropical plants in multiple shelters, and the potential distribution areas predicted by many plants in the last glacial period have not completely retreated to the south of 24° N [49]. During the LGM, the total suitable area contracted significantly in the southeast (Figure 6). The Korean Peninsula and Japan were high-suitability areas for *P. densiflora*, and the areas had little change in different periods (Figure 5). The overlapping areas of the past models and the current distribution may suggest a refuge area with rich genetic diversity [50–52]. Moreover, the mountainous area itself has a high topographic heterogeneity, maintains a high species diversity and uniqueness and is usually an important refuge for animals and plants. Therefore, it can be inferred that the *P. densiflora* population did not retreat southward on a large scale during the LGM. It is likely to have survived in the refuge formed by the complex mountainous terrain and mild microenvironment of Japan and the Korean Peninsula. It has not been adversely affected or restricted by the ice age, so it can also be speculated that Japan may be the origin of *P. densiflora*.

Many studies have shown that climate warming may reduce the potential distribution area of species [53,54]. Compared with the last glacial period, the climate in the mid-Holocene was warmer and wetter. The total suitable area was increased, but the highsuitability area had little change (Figure 5, Table 3). The reason is that *P. densiflora* is a species with a wide distribution range and strong ecological adaptability, which is related to a variety of environmental conditions in this area [24]. In a certain range, global warming can affect precipitation, accelerate the phenological process and prolong the growth season [55]. This study showed that the potential geographical distribution of *P. densiflora* under the two emission scenarios in the future will be significantly reduced compared with the current distribution area (Table 3), resulting in fragmentation (Figure 5). It showed that the future climate warming will have certain negative impacts on the growth of *P. densiflora*, and the habitat reduction of *P. densiflora* in the future will be much greater than that in the historical period. The distribution area will shrink significantly in the southeast, and the suitable areas in the southeast coast of Russia will increase significantly. The high-suitability areas will still be concentrated in Japan, the Korean Peninsula, Liaodong Peninsula and Shandong Peninsula (Figures 5 and 6), indicating the strict requirements of *P. densiflora* to the temperature and precipitation range.

Research has shown that global climate change leads to the continuous rise of global temperature, precipitation mode (time and space) and precipitation intensity [56]. More than half of the research objects may be threatened by the 2080s, assuming that the species cannot spontaneously spread in Europe [7]. As a result, many species will migrate with global warming [6,57,58]. The results of this study showed that the distribution center of *P. densiflora* changes to a small northward migration from current to the future climate scenario. It showed the trend of north-south migration between the glacial and non-glacial periods (Figure 7). It is probably due to the formation of glaciers in the high-altitude and high-latitude areas under the glacial climate scenario that the species migrated to low-latitude and low-altitude areas. After entering the Holocene, the glaciers melted, and the species migrated to the high-altitude area with the continuous increase of temperature [59]. In short, the total suitable area of *P. densiflora* is different in different periods, but the high-suitability area is stable. It showed that *P. densiflora* had strong adaptability to climate change and had no extreme regression due to severe climate fluctuations. *P. densiflora* still had a broad and suitable natural habitat.

5. Conclusions

Estimating how climate change will affect the distribution of *P. densiflora* species is of vital importance for conservation. Herein, the MaxEnt model was used to identify a wide suitable habitat for *P. densiflora*. The suitable habitat for *P. densiflora* in East Asia was about 3.62×10^6 Km². The Bio18, Bio14, Bio1 and Bio8 climatic factors were 650–800 mm, 900–1050, 10–13 °C and 23–24 °C in the high-suitability distribution area, respectively. From the past to the future, the distribution area showed a single peak trend, and the current distribution area was the largest. Under the different climate scenarios, the distribution center of *P. densiflora* showed the trend of north-south migration between the glacial and non-glacial periods. Under the future climate scenarios, the potential habitat range of *P. densiflora* may increase fragmentation, which will have significant negative impacts on the habitat of *P. densiflora*. *P. densiflora* plays an important role in the stability of the local

ecosystem. Therefore, this research can provide a scientific basis for the response to climate change and the protection and management of habitat.

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