

Modeling Habitat Suitability of *Hippophaerhamnoides* L. Using MaxEnt under Climate change in China: A Case Study of *H. r. sinensis* and *H. r. turkestanica*

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Abstract

Hippophaerhamnoides is widely known for its important ecological, economic, and social benefits. It is known as the pioneer plant of soil and water conservation, with homology in food and medicine. Here we used occurrence data and environmental (climate and soil) variables to simulate and predict the habitat distribution for *H. r. sinensis* and *H. r. trkestanica* in China, both at the current time and in the 2050s (2041-2060). Our aim was to analyze the dominant factors effecting its distribution using MaxEnt and the spatial analysis of geographic information system. The results indicated that *H. r. sinensis* is mainly distributed in Shaanxi, Shanxi, Sichuan, Qinghai, Gansu, Ningxia, Tibet, and Inner Mongolia, and is mainly affected by bio13 (precipitation of the wettest month), bio11 (mean temperature of the coldest quarte) and bio3 (Isothermality). The suitable habitat of *H. r. trkestanica* is mainly distributed in Xinjiang, and Tibet, and is mainly affected by bio13 (precipitation of the wettest month), bio2 (mean diurnal range) and bio15 (precipitation seasonality). Although, the two subspecies tend to expand and migrate toward lower latitude under future climate scenarios, there are some differences. *H. r. sinensis* will migrate westward, while *H. r. trkestanica* will migrate eastward as a whole. They have a high stability of suitable habitat and are not at risk of extinction in the future. The study's findings help to clarify the resource reserve of *Hippophaerhamnoides* L. in China, which will help to guide the protection of wild resources and to popularize artificial planting in suitable areas, and provides scientific basis for the protection of ecological environment.

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Abstract: *Hippophaerhamnoides* is widely known for its important ecological, economic, and social benefits. It is known as the pioneer plant of soil and water conservation, with homology in food and medicine. Here we used occurrence data and environmental (climate and soil) variables to simulate and predict the habitat distribution for *H. r. sinensis* and *H. r. trkestanica* in China, both at the current time and in the 2050s (2041-2060). Our aim was to analyze the dominant factors effecting its distribution using MaxEnt and the spatial analysis of geographic information system. The results indicated that *H. r. sinensis* is mainly distributed in Shaanxi, Shanxi, Sichuan, Qinghai, Gansu, Ningxia, Tibet, and Inner Mongolia, and is mainly affected by bio13 (precipitation of the wettest month), bio11 (mean temperature of the coldest quarte) and bio3 (Isothermality). The suitable habitat of *H. r. trkestanica* is mainly distributed in Xinjiang, and Tibet, and is mainly affected by bio13 (precipitation of the wettest month), bio2 (mean diurnal range) and bio15 (precipitation seasonality). Although, the two subspecies tend to expand and migrate toward lower latitude under future climate scenarios, there are some differences. *H. r. sinensis* will migrate westward, while *H. r. trkestanica* will migrate eastward as a whole. They have a high stability of suitable habitat and are not at risk of extinction in the future. The study's findings help to clarify the resource reserve of *Hippophaerhamnoides L.* in China, which will help to guide the protection of wild resources and to popularize artificial planting in suitable areas, and provides scientific basis for the protection of ecological environment.

Keywords: Environmental variables; Climate change scenarios; Maximum entropy (MaxEnt) model; suitable habitat; centroid migration

Cover Letter

Dear editor:

We are submitting a manuscript entitled “Modeling Habitat Suitability of *Hippophaerhamnoides L.* Using MaxEnt under Climate change in China: A Case Study of *H. r. sinensis* and *H. r. turkestanica*” for your consideration for publication as a communication in Ecology and Evolution. This article investigated the changes of the geographical distribution for *Hippophaerhamnoides L.* under climate change, which is studied mainly because: (1)

Hippophaerhamnoides is widely known for its important ecological, economic, and social benefits. However, as the climate has warmed in recent years, the numbers of this species and countries with this plant have decreased steadily; (2) at present, there are many studies on *Hippophaerhamnoides*, but less attention is paid to the changes in its geographical distribution under climate change; (3) in this study, we found that two subspecies of *Hippophaerhamnoides L.* (*H. rhamnoides. Sinensis* and *H. rhamnoides. Turkestanica*) tend to expand and migrate toward lower latitude under future climate scenarios, there are some differences. *H. r. sinensis* will migrate westward, while *H. r. trkestanica* will migrate eastward as a whole. They have a high stability of suitable habitat and are not at risk of extinction in the future in Chian. (3) this study's findings help to clarify the resource reserve of *Hippophaerhamnoides L.* in China, which will help to guide the protection of wild resources and to popularize artificial planting in suitable areas, and provides scientific basis for the protection of ecological environment.

The topic of this manuscript meets the scope of the journal and the study will be of interests to a wide range of readers. We confirm that neither the manuscript nor any parts of its content are currently under consideration or published in another journal. And all authors have approved the manuscript and agree with its submission to Ecology and Evolution.

Thank you for receiving our manuscript and considering it for review. We appreciate your time and look forward to your response.

Yours sincerely

31 May 2022

Author: Xiao-hui HE

INTRODUCTION

Global climate change has become the most important environmental issue and the most urgent challenge we have ever faced. It is considered one of the major threats to global biodiversity in the 21st Century (Dawson, 2011; Zhao et al., 2021). Climate change affects significantly the growth, reproduction and habitat of species, plant phenology, and even the ecosystem stability, both directly and indirectly (Pielke et al., 1998). Additionally, changes in the vegetation structure affect the exchange of substances and energy, such as carbon and water, between the atmosphere and land surface, and will subsequently lead to changes in regional climates (Bakkenes et al., 2002). If the climate and environment change dramatically, many species will not be able to survive, and some rare plants will face the risk of extinction (Diversity, 2010). Nearly one-quarter of plant species are at risk of extinction according to the Global Biodiversity Outlook 3 (GBO-3) report (Bellard et al., 2012). Therefore, biodiversity conservation, geographical distribution, and migration of species under climate change have become hot topics in botany, geography and ecology research in recent years (Guo et al., 2016; Yi et al., 2016; Guan et al., 2018; Ab Lah et al., 2021).

In recent years, with advances in statistics, a number of statistical and computer-based methods have been used to assess the distribution of suitable habitat for various species (Elith et al., 2011). Species distribution models (SDMs) are one of the most important tools for ecology and biogeography, providing the classical methods for combining niche factors with specific species (Guisan and Thuiller, 2007). SDMs mainly use environmental data and species distribution data (presence or absence) to analyze the relationship between environment and species, estimate species' niches, and then predict species' habitat preferences in the form of a probability using various machine learning algorithms (Guisan and Thuiller, 2007; Elith et al., 2011). The common algorithms of SDMs include: GAM, GLM, DoMain, BioMapper, BioClim, CliMex, MaxEnt, and so on (CARPENTER et al., 1993; Hirzel and Guisan, 2002; Guan et al., 2018). Although a variety of models are available for predicting geographic distribution, Maximum entropy (MaxEnt) model provides higher predictive accuracy with less or limited data, and performance well (Elith et al., 2006; Ghareghan et al., 2020). The input species data can be presence-only data and the MaxEnt simulation results can directly generate spatial habitat suitability maps (Phillips and Dudik, 2008; Elith et al., 2011). Therefore, MaxEnt is not only commonly used for the determination of the geographical distribution of plant species (Guan et al., 2018; Li et al., 2020), but also widely used in other fields, such as identifying suitable habitat for animals (Su et al., 2021), biological invasion (Gallagher et al., 2010), urban geography and archaeology (Muttaqin et al., 2019), space-generating capacity of natural hazards (Javidan et al., 2021), and energy suitability distribution (Tekin et al., 2021).

Hippophaerhamnoides (Elaeagnaceae Juss., *Hippophae* L.), also known as sea buckthorn, is a flowering shrub or small tree. It first appeared from the eastern Himalayas to the Hengduan Mountains, and it has a tendency to grow in the arid, semi-arid and high mountainous ecosystems of Asia and Europe, including China, Russia, Mongolia, India, Finland, France, Nepal, Iran, Pakistan, Afghanistan, Pakistan, Kazakhstan, Bhutan, Britain, Germany, Norway and Sweden (Ui Haq et al., 2021). This genus contains seven species and eleven subspecies around the world, with seven species and seven subspecies in China (Swenson and Bartish, 2002). *Hippophaerhamnoides* is most abundant in China, being widely distributed in southwest, northwest, and northern China (Suryakumar and Gupta, 2011; Lian, 2000). *Hippophaerhamnoides* is received attention from scholars in different fields all around the world because of its ecological value in soil and water conservation, windbreak and sand fixation, pharmacological effects in treating human diseases and improving skin, and its economic food, feed and fuel value (Suryakumar and Gupta, 2011; Zielinska and Nowak, 2017; Pundir et al., 2021). Studies on *Hippophaerhamnoides* have mainly focused on its biochemical characteristics, genetic structure, pharmacological actions, germplasm resources and phylogeography (Zielinska and Nowak, 2017; Pundir et al., 2021; Ui Haq et al., 2021). However, little attention has been paid to its geographical distribution or its response to climate change.

The Global Biodiversity Information Facility (GBIF) stated that Eurasia is a hot spot of the suitable growth of *Hippophaerhamnoides*. However, as the climate has warmed in recent years, the numbers of this species and countries with this plant have decreased steadily (Pundir et al., 2021). Understanding the spatial distribution of habitat suitable for *Hippophaerhamnoides* with continued climate change not only provides theoretical support for the protection of wild species and artificial planting, but also provide a scientific basis

for protecting the ecological environment.

In this paper, we considered *H. rhamnoides. Sinensis* (*H. r. sinensis*) and *H. rhamnoides. Turkestanica* (*H. r. turkestanica*) due to their large number in terms of the distribution of each subspecies of *Hippophae rhamnoides* L.. As our research aims, we mainly focused on the following: questions (1) How do environmental factors affect the spatial distribution of *H. r. sinensis* and *H. r. turkestanica*? (2) What is the habitat suitable for these species in China under the current and future climate scenarios? (3) How do their suitable habitat and centroid change under the different climate scenarios?

MATERIALS AND METHODS

Data sources

Occurrence data

The occurrence data of *H. r. sinensis* and *H. r. turkestanica* in China were obtained from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>), the National Specimen Information Infrastructure (NSII, <https://nsii.org.cn/>), the Chinese Virtual Herbarium (CVH, www.cvh.ac.cn/) and the China National Knowledge Infrastructure (CNKI, After removing the repeated, invalid, and wrong data, 232 occurrence data of *H. r. sinensis* and 73 occurrence data of *H. r. turkestanica* were obtained to build the model (Figure 1).

Figure 1. Sample sites of *H. r. sinensis* and *H. r. turkestanica* populations in China. Provinces names are abbreviated, X

Environment variables

Bioclimatic variables are of biological significance in determining the environmental niche of species (Yi et al., 2016). A total of 36 environmental variables were selected from three types (19 climate variables and 17 soil variables) in this study. The climate data were downloaded from WorldClim version 2.1 (<http://www.worldclim.org/>), including 19 bioclimatic variables (Bio1–Bio19) (Fick and Hijmans, 2017). The 19 variables were derived from the monthly temperature and rainfall values of meteorological stations around the world from 1970 to 2000, to generate more biologically meaningful variables; this is a popular dataset used in species distribution modeling and related ecological modeling techniques (Zhao et al., 2021). The future climate variables of the 2050s (2041–2060) were simulated by Beijing Climate Center Climate System Model version 2 (BCC-CSM2-MR) for representative concentration pathway (SSP126, SSP245, SSP370, and SSP585) (Fischer et al., 2005; Zhao et al., 2021). Soil data were obtained from the Harmonized World Soil Database (HWSD). The data resolution is 2.5 minutes resolution (also referred to as ~ 5 km spatial resolution).

Environmental variables are characterized by complexity, comprehensiveness, and correlation. In order to reduce the collinearity between variables, which leads to the over-fitting of a model, and to ensure the precision of model simulation, we screened the environmental variables before the simulation. First, all environmental variables were input the MaxEnt model for simulation, and any with a contribution rate of 0 were removed (Worthington et al., 2016); Second, the correlation analysis was performed in ENMTTools. Finally, for a set of variables ($|r| \geq 0.8$) (Wei et al., 2018), we removed one variable that contributed less in the initial modeling. In the end, we selected 10 variables for *H. r. sinensis* and 11 variables of *H. r. turkestanica* in the modeling (Table 1).

Methods

Model operation and evaluation index of model accuracy

The 232 occurrence data of *H. r. sinensis* and 10 environmental variables were imported into MaxEnt 3.4.1 for modeling operation; for the 73 occurrence data of *H. r. turkestanica* and 11 environmental variables data, we performed the same operation. In this research, we randomly selected 75% of occurrence data as the training set to establish models, and the remaining 25% was used as the testing set and to verify the accuracy of the

simulation (Guo et al., 2016). The contribution of each variable to the species distribution was calculated by using the jack-knife test. Furthermore, a threshold rule of 10 percentile training presence was applied. We used the area under the receiver operating characteristic (ROC) curve (AUC) as the evaluation indicator of the accuracy of the MaxEnt model because the AUC is not affected by the choice of threshold (Vanagas, 2004; Peterson et al., 2008). The ROC curve is a graphical method that uses multiple thresholds to show the relationship between false positive ratio (1 minus the-specificity) and sensitivity (Zhang et al., 2020; Fang et al., 2021). The AUC values range between 0 and 1. An AUC value of < 0.5 indicates that the model fails to describe reality, 0.5 indicates pure guessing, 0.5–0.6 indicates failure, 0.6–0.7 indicates poor performance, 0.7–0.8 indicates fair performance, 0.8–0.9 indicates good performance, and values of 0.9–1 indicate excellent performance (Swets, 1988).

Suitable habitat grade classification and Spatial variation

The range of each raster value was 0–1, which represents the fitness probability of the species in the study area. The habitat suitability predictions were classified into three grades based on the Jenks algorithm.

As climate changes, the habitats of species will also change. Species distribution models can be used to track and simulate these changes. The probability distribution maps of *H. r. sinensis* and *H. r. turkestanica* were converted into binary maps, where 0 represents an unsuitable habitat and 1 represents a suitable habitat. The future and current binary maps were calculated in the grid calculator in ArcGIS, then we generated the spatial change map of the two subspecies from one species under different climate scenarios in the future compared to the current scenario. In the map, 0 is an unsuitable habitat for both current and future climate scenarios, 1 indicates a suitable habitat lost in the future, 2 denotes a newly suitable habitat in the future, and 3 indicates a suitable habitat stable that will remain so in the future.

The centroid is an important index used to describe the spatial distribution of a species. Its changes can reveal the spatial aggregation and migration of species in a certain period of time. The determination of the suitable habitats' centroid to be done in ArcGIS. First, maps should be converted into vectors and the points representing the suitable habitat should be filtered out. Subsequently, the raster centroid was simulated and converted into a point. Finally, the coordinates of the suitable habitats' centroid were calculated. In this way, we were able to use the centroid change under different climate scenarios to indicate the spatial pattern change of

Hippophaerhamnoides L.

RESULTS

Model accuracy evaluation and variables' contribution

Model accuracy evaluation

After the environmental variables were selected and the model simulation, the mean AUC values of *H. r. sinensis* and *H. r. turkestanica* were 0.927 (**Figure 2a**), and 0.969 (**Figure 2b**), and the AUC standard deviation were 0.004 and 0.009, respectively.

Figure 2. Receiver operating characteristic (ROC) curves of (a) *H.r.sinensis* and (b) *H.r.turkestanica*.

Variables' contribution and response to suitability

The contribution rate of each environmental variable is shown in Table 1. And they are average value over replicate runs. For *H. r. sinensis*, the top five environmental variables contributing to species distribution were precipitation of the wettest month (bio13, 28.83% contribution rate), mean temperature of the coldest quarter (bio11, 25.33%), isothermality (bio3, 18.54%), topsoil calcium carbonate fraction (t-caco3, 9.60%) and precipitation seasonality (bio15, 8.03%), their cumulative contribution was 90.33%. For *H. r. turkestanica*, the top six environmental variables contributing to species distribution were precipitation of the wettest month (bio13, 18.59% contribution rate), mean diurnal range (bio2, 13.49%), precipitation season-

ality (bio15, 11.9%), topsoil cation exchange capacity of soil (t-cec-soil, 10.51%), topsoil calcium carbonate fraction (t-caco3, 10.31%), and topsoil ph (h2o) (t-ph-h2o, 7.22%), their cumulative contribution was 71.21%.

Based on this, we suggested that climatic elements have more influence on the growth of these two subspecies of *Hippophaerhamnoides* L. than soil elements, especially *H. r. sinensis*. The first three dominant factors were all climatic elements, and the relationships between key variables and species suitability distribution were investigated by making their response curves.

According to the response curves, for *H. r. sinensis*, we found that the highest habitat suitability was obtained when bio13 ranges from 87mm to 135mm. And the relationship between habitat suitability and bio13 showed a positive skewness distribution, with the estimated peak value of 106mm (**Figure 3a**). When a location has a value above or below this value, its suitability decreases rapidly. At the same time, the habitat suitability value is high when bio11 ranges from -9.35-0.37 to -0.37. Beyond this range, the suitability declines rapidly, the curve is almost normally distributed (**Figure 3b**). Surprisingly, the response curve of bio3 and habitat suitability is bimodal, with an increasing suitability index in the range between 28.3 and 31.9, 41.5 and 45.3 (**Figure 3c**).

We found that the three key environmental variables affecting the distribution of *H. r. turkestanica* are bio13, bio2, and bio15, with values of 0mm – 57mm (**Figure 4d**), 12.6 - 14.9 (**Figure 4e**), and 12.1 - 79.5 (**Figure 4f**), respectively. Its habitat suitability is positively skewed with bio13 when values are higher or lower than the peak, which is 3.5mm. Its suitability decreases sharply with the increase in bio13. We found that it has a narrow niche overall, its adaptability becomes poor beyond this range. The relationship between its suitability and bio2 could be approximately described as a negative distribution. Bio15 has a large adaptation range, and the probability of species growth decreases with increasing the value of bio15.

Figure 3. Response curves of probability of presence of (a-c) *H. r. sinensis* and (d-f) *H. r. turkestanica*.

Habitat suitability under current and future climate scenarios

Habitat suitable for *H. r. sinensis* under the current and future climate scenarios

The distribution maps of the habitat suitable for *H. r. sinensis* under the current and future climate scenarios be shown in Figure 4. The results showed that the suitable area is $883.19 \times 10^3 \text{ km}^2$ in the current climate scenario, which accounts for 9.20% of the land area of China (**Table 2**). The species is mainly located in the Loess Plateau and the marginal area from southeast to northeast of the Qinghai-Tibet Plateau. It is distributed in a belt from southwest to northeast, including most areas of Shanxi, central and northern Shaanxi, southwestern Sichuan, Ningxia, southern and eastern Gansu, northeastern Qinghai, central Inner Mongolia, and southeastern Tibet (**Figure 4a**). The low-suitability area is mainly distributed around the suitable area, covering approximately $1444.01 \times 10^3 \text{ km}^2$, accounting for 15.04% of the studied area. Under the different climate scenarios in the 2050s, the distribution of the suitable habitat is similar to the current distribution (**Figure 4b-e**), but the area shows an increasing trend overall, by 150.57×10^3 , 239.35×10^3 , 246.35×10^3 , and $233.78 \times 10^3 \text{ km}^2$ under SSP126, SSP245, SSP370, and SSP585 scenarios, respectively. The average suitable habitat area is $1100.71 \times 10^3 \text{ km}^2$ in the 2050s, accounting for 11.47% of the study area, which is $217.52 \times 10^3 \text{ km}^2$ more than the current area. The unsuitable habitat areas decrease (**Table 2**).

Figure 4. The habitat suitable for *H. r. sinensis* in China both (a) currently and in the 2050s, under the (b-e) scenarios S

Habitat suitable for *H. r. turkestanica* currently and under future climate scenarios

The distribution map of habitat suitable for *H. r. turkestanica* under the current and future climate scenarios is shown in **Figure 5**. The results showed that the currently suitable habitat area is $227.15 \times 10^3 \text{ km}^2$, accounting for 2.37% of the land area of China (**Table 2**). The habitat is mainly located around the Tarim

Basin and Jungar Basin in Xinjing, which include Hotan, Kashgar, Kizilsu Kirgiz, Aksu, Ili Kazak, Bortala Mongolian, Tacheng, tulufan, and Altay, etc.; western Ali, Shigatse and Qamdo in Tibet; Haixi Mongolian and Tibetan Autonomous Prefecture in Qinghai; Ganzi and Aba prefectures in Sichuan, and parts of Gansu and Ningxia (**Figure 5a**). The low-suitability areas are also mainly distributed around the suitable area, covering an area of approximately $1172.39 \times 10^3 \text{ km}^2$, accounting for 12.21% of the study area. Under the different climate scenarios in the 2050s, the changes in habitat distribution occur for suitable and low-suitability habitat (**Figure 5b-e**). The suitable habitat area mainly shows an increasing trend under future climate scenarios with particularly significant changes under SSP126. The average suitable habitat area is $414.97 \times 10^3 \text{ km}^2$ in 2050s, accounting for 4.32% of the study area, which is $187.82 \times 10^3 \text{ km}^2$ more than the current area. The area of low-suitability habitat also increases, about $151.71 \times 10^3 \text{ km}^2$ (**Table 2**).

Figure 5. The habitat suitable for *H. r. turkestanica* in China (**a**) currently and in the 2050s under the (**b-e**) scenarios SS

Spatial pattern changes in the suitable habitat under different climate scenarios

Spatial change in suitable habitat

The results were calculated by a grid calculator and are shown in Figure6. Under the different future climate scenarios, significant dynamic changes occur (gain, loss, or stable habitat) for both *H. r. sinensis* and *H. r. turkestanica* compared to the current climate scenario. The suitable habitat to be lost by *H. r. sinensis* is mainly distributed in Hebei, Shangdong and Henan. However, some areas in eastern Inner Mongolia will experience a decrease in suitability rating under the SSP585. The areas of increased suitability are mainly distributed in Tibet, Qinghai, and Inner Mongolia, and with the increase of emission concentration, a belt area is formed in Inner Mongolia from southeast of Alxa left banner to southwest of Hailar.

In the future, the habitat gained by *H. r. turkestanica* is mainly distributed around the Jungar Basin, Altay and Tacheng, the Tianshan Mountains, and Turpan Basin in Xinjiang, central Changdu in Tibet, Western and central of Inner Mongolia, Jiuquan in Gansu, southwest of Sichuan. Under SSP245, the area of suitable habitat increased the most, and mainly in Xinjiang. These are the main loss areas of suitable habitat, such as Xifeng in Gansu, Yulin and Yanan in Shaanxi, and the southern of Shanxi.

The habitats suitable for these two subspecies are relatively stable. The percentage of the stable suitable habitat for *H. r. sinensis* slightly higher than that for *H. r. turkestanica*: the average value of the former is 79.06%, and the value of latter is 76.90 (**Table 3**). The results showed that the change in habitat area of the two subspecies from one species are slightly different under the different scenarios. The stability of suitable habitat for *H. r. sinensis* will show a slight decrease trend as the concentration of gas emissions increases. While *H. r. turkestanica* will be the least stable under SSP245, and the most stable under SSP126.

Figure 6. Changes in the habitat suitable for (a-d) *H. r. sinensis* and (e-h) *H. r. turkestanica* under different climate char

Migration of centroid of suitable habitat

Figure 7 shows that the straight-line direction and distance of geographic migration of the suitable habitat centroids are heterogeneous. Currently, the centroid of suitable habitat is located at $106^\circ 02' 32'' \text{E}$, $35^\circ 44' 09'' \text{N}$, in Guyuan county in southern Ningxia. While the centroids will gradually migrate westward with increasing emission concentrations under different future climate scenarios, and are distributed in Dingxi county, Linxia county and Xiahe county in southeastern Gansu. Under the SSP126, SSP245, SSP370 and SSP585, the centroids are located at $104^\circ 09' 10'' \text{E}$, $35^\circ 31' 30'' \text{N}$; $103^\circ 27' 16'' \text{E}$, $35^\circ 26' 0.5'' \text{N}$; $103^\circ 08' 20'' \text{E}$, $35^\circ 07' 55'' \text{N}$; and $102^\circ 23' 50'' \text{E}$, $34^\circ 51' 50'' \text{N}$, respectively (**Figure 7a**). Overall, *H. r. sinensis* may migrate to the lower latitudes in the future.

The centroids of *H. r. turkestanica* are located in Qiemo county, southeast Xinjiang. Currently, the centroid is located at $85^\circ 43' 41'' \text{E}$, $38^\circ 21' 26'' \text{N}$. Under the SSP126, SSP245, SSP370, and SSP585 scenarios, the

centroids move to 85deg15'26"E, 38deg11'51"N; 87deg01'55"E, 38deg50'42"N; 86deg41'21"E, 37deg40'31"N, and 86deg20'23"E, 38deg11'09"N respectively. Except for the centroid of the SSP245 scenario, which migrates to the higher latitude, the others migrate to the lower latitude (**Figure 7b**). The main migration direction will towards eastern, and the magnitude of migration is greater under SSP245 and SSP370.

Figure 7. The centroid migration of suitable habitats of (a) *H. r. sinensis* and (b) *H. r. turkestanica*.

DISCUSSION

Model accuracy and main environment variables

Although many methods can be used for understanding a species' ecological niche distribution and for predicting the potential suitable habitat, the single model is still widely used. Among the SDM studies, MaxEnt is more effective in simulating the habitat suitability of plant species (Cobben et al., 2015; Ghareghan et al., 2020; Ab Lah et al., 2021b). So, we chose this method for our study. The results showed that MaxEnt model can effectively simulate and predict the habitats suitable of *Hippophae rhamnoides* L. Therefore, we determined that the conclusions of this study are reliable. MaxEnt also used to study the suitable distribution of *H. r. sinensis* by Liu and Huang, who showed that the model achieved good simulation accuracy (Liu, 2016; Huang et al., 2018). Despite MaxEnt having many advantages, some scholars think that a single model can produce over-fitting, and an integrated model may reduce the uncertainty of model fitting (Battini et al., 2019). The ensemble model (EM) strategy is widely used for studying the habitat distribution of species because of its higher accuracy, and better universality and fitting (Guo et al., 2019; Zhao et al., 2021). Moreover, MaxEnt is only applicable when considering abiotic factors; its applicability to areas strongly affected by human activities needs to be further verified. In future studies, other factors potentially effecting the distribution of species, such as human activities, biological interactions, diffusion constraints, and so on, should be more comprehensively considered.

We found that bio13, bio11, and bio3 are the most important factors affecting the distribution of *H. r. sinensis*. This is consistent with the findings of many studies. For example, *H. r. sinensis* is affected by precipitation and temperature, and is less affected by soil, so it can be grown in meadow soil, chernozem, sandy soil and even in half-stone, sandstone, and sandy soil areas (Liu, 2016). The annual precipitation has a significant effect on its distribution: the 400 mm contour is the dividing line of the distribution area of *H. r. sinensis* on the Qinghai-Tibet Plateau (Lian, 2000). The Yunnan-Guizhou Plateau is unsuitable for its growth because its precipitation is too much, which is beyond the suitable range, so it does not extend to this area, which contradicts the research conclusion of Li (Li et al., 2015). Whereas, Huang found that the precipitation of the coldest quarter has an important effect, the effect of this variable was not obvious in our study (Huang et al., 2018). Precipitation and temperature are still the dominant factors affecting the geographical distribution of *H. r. turkestanica*. Its range of suitable habitat is narrower than that of *H. r. sinensis*, but its requirement for bio 13 is lower than that of *H. r. sinensis*, which may be the reason why the area of habitat suitable for *H. r. turkestanica* smaller than that of *H. r. sinensis*. *H. r. turkestanica* grows more easily under extreme drought conditions than *H. r. sinensis*. In addition, the response curves between species suitability and dominant factors show mainly a positive skew relationship (Austin, 1987; Zhang, 2018). We found that the suitability is basically a skewed relationship with dominant factors, but not always positively biased.

In this study, we did not consider the terrain variables such as landform classes, hill shade, heat load index, compound topographic index (Driver, 2020), at the same time, other factors potentially effecting the distribution of species, such as human activities, biological interactions and diffusion constraints. Thus, if we consider the factors more comprehensively in the next step, the results will be more accurate and the suitable habitat may be more fragmented.

Distribution of currently suitable habitats

Climate change has important impacts on shift in the distribution ranges of many terrestrial organisms. Under the current climate scenario, the habitat suitable for *H. r. sinensis* is concentrated in the middle and upper reaches of the Yellow River, the Loess Plateau, and the northeastern to southeastern margin of the Qinghai-Tibet Plateau, from the northeast of Hengduan Mountains to Taihang Mountains, north of Qinling Mountains and south of Yinshan Mountains, and it is distributed in a belt from southwest to northeast (**Figure 4, Table 2**). The results are similar to those of Liu, but slightly differ due to the differences in the number of selected sampling points and the suitability classification criteria applied (Fischer et al., 2005). By field investigation, we found that this subspecies likes sunlight and has certain water resources requirements, and distributes on banks of rivers, mountains, and valleys, and grows well in sparse forest land (Fischer et al., 2005). According to the difference in the climate and vegetation zonality in different growing areas of *H. r. sinensis* in China, four typical distribution areas can be identified: the Western Sichuan Plateau and Qinba Mountain distribution area, the Southern Loess Plateau distribution area, the central and northern Loess Plateau and Mu Us sandy land and arsenic sandstone distribution area, and the Qinghai Plateau distribution area (Dai et al., 2011). This subspecies can grow in the arid and barren Loess Plateau and arsenic sandstone areas due to its strong root germination and rich rhizobia, which can continuously improve the soil texture through nitrogen fixation. As a primitive group of *Hippophae*, *Hippophae rhamnoides* originated from the Qinghai-Tibet Plateau, some scholars have speculated that it may have spread from northeast to northwest and north China along the Hengduan Mountains (Lian, 2000). In the mid-1960s, *H. r. sinensis* invaded Mu Us sandy land through birds, and occupied the habitat with good water conditions in the area, and rapidly diffused to the slope and top of sand dunes, then formed a local unique ecological barrier. In recent years, *H. r. sinensis* has cultivated in Heilongjiang, Jilin, Shandong, Henan, and Beijing.

Under the current climate scenario, the area of habitat area suitable for *H. r. turkestanica* for 2.37% of the total territory of China, which is mainly distributed in Xinjiang, Tibet, and Gansu (**Figure 5, Table 2**). A small amount of artificial cultivation occurs in Qinghai, Ningxia, and Inner Mongolia. It is often found in River Valley terraces, floodplains, and open hillsides. There are banded natural communities in the Tahe River Basin of Southern Xinjiang, along the Hotan River, bortara River Valley, both sides of the river in the Ali Region of Tibet, and Danghe river of Gansu (Han, 2010). In addition, it shows drought resistance and barren resistance, and can grow in saline alkali beach and desert. For example, natural *H. r. turkestanica* grows in Taklimakan Desert. The two subspecies studied in this paper do not have high soil requirements, but some researchers showed that the growth of *H. r. turkestanica* is not as good as that of *H. r. sinensis* under the arsenic sandstone conditions (Han, 2010).

Spatial changes in suitable habitats under future climate scenarios

Different regions have will experience climate change mechanisms and impacts on species. The changes that will occur the various species under different climate scenarios are also heterogeneous (Dyderski et al., 2018). Therefore, with climate warming, species migrate to areas suitable for their growth, which will not be harmful to all species. The range of suitable habitats for most species will be reduced and a few will expand (Li et al., 2013; Bezeng et al., 2017; Dyderski et al., 2018). There is no general tendency for even closely related plants in the respond to climate change (Kolanowska et al., 2017). For the two subspecies considered in this study, the predicted range of suitable habitat under different climate scenarios in the future is basically consistent with the currently suitable habitat range, but shows significant dynamic changes, with some differences. Their suitable habitat showed an increasing trend in the future climate scenario. The question of whether the response of subspecies to climate change can reflect the characteristics of the whole species needs to be further explored.

In addition, the area of stable habitat for most species under the future climate scenario was previously found to account for more than 60% of the current suitable area (Zhang, 2018), which means that the area suitable for most species is generally stable and will not face the risk of extinction due to climate warming. Here, we obtained a similar conclusion. These subspecies are not at risk of extinction in the future, and *H. r. turkestanica* is more vulnerable to climate change than *H. r. sinensis*.

The suitable habitat range, the direction and distance of centroid migration of these subspecies were hetero-

geneous under different climate scenarios (**Figure 5-7**). The shrinking areas of *H. r. sinensis* are mainly in Tibet, Qinghai, Gansu and Inner Mongolia, the suitable growth areas are formed a belt in Inner Mongolia. The centroids of suitable habitat will move to the lower latitudes in the future and gradually migrate westward with increasing emission concentrations. *H. r. turkestanica*'s change also showed the same trend under the four climatic scenarios in the future, and its suitable range will increase compared to the current, and the centroid will move to the eastern and lower latitude overall. Under the trend of global warming, the area of arid and semi-arid areas will gradually increase (Huang et al., 2016). This may also be the reason for the expansion of suitable habitat of *H. r. turkestanica* in the future. Nevertheless, many studies had shown that most species will migrate to high altitude in order to avoid the rapid warming of low altitude and low latitude habitats (Hu and Liu, 2014). The findings of this study do not support the view. The conclusion of this study is different with above viewpoint because of the different species studied.

CONCLUSION

In this study, we successfully modeled the habitat suitability of *H. r. sinensis* and *H. r. turkestanica* under the current and future climate change scenarios using MaxEnt. Our results showed that they prefer to grow in arid and semi-arid areas. *H. r. sinensis* is mainly affected by bio13, bio11 and bio3. *H. r. turkestanica* is mainly affected by bio13, bio2 and bio15, and is more suitable for growing in the extreme arid area, due to its requirement of annual precipitation is lower than that of *H. r. sinensis*. The two subspecies' habitat have obvious differences. However, the changing trend is towards expansion and the centroids of suitable habitat will migrate toward lower latitudes under future climate scenarios. Their distribution could also be affected by the river, so the modeling result could be improved adding this variable in the future. *Hippophae rhamnoides* Linn., as a multi-purpose tree species, plays an important role in the protection and restoration of ecological environment in China. Therefore, this study is helpful to the protection of wild resources and the expansion of artificial cultivation, and provides a scientific reference for eco-environmental managers.

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Table 1. Environment variables used for modeling the habitat suitability distribution of *H. r. sinensis* and *H. r. turkestanica* and variables' contribution

Species	Environment variables(Abbreviation)	Description	Contri
<i>H. r. sinensis</i>	bio3	Isothermality	18.54
	bio5	Maximum temperature of the hottest month ()	4.89
	bio11	Mean temperature of coldest quarter ()	25.33
	bio13	Precipitation of wettest month (mm)	28.83
	bio15	Precipitation seasonality	8.03
	t.caco3	Topsoil calcium carbonate fraction (% weight)	9.60
	t.gravel	Topsoil gravel fraction (%vol.)	1.27
	t-ece	Topsoil salinity (dS/m)	0.60
	t.sand	Topsoil sand fraction (% weight)	0.60
	t.ph-h2o	topsoil PH (h2o)	2.31
<i>H. r. turkestanica</i>	bio2	Mean diurnal range ()	13.49
	bio7	Temperature annual range ()	5.75
	bio11	Mean temperature of coldest quarter ()	6.09
	bio13	Precipitation of wettest month (mm)	18.59
	bio15	Precipitation seasonality	11.92
	t.cec_soil	Topsoil cation exchange capacity of soil	10.51
	t.caco3	Topsoil calcium carbonate fraction(% weight)	10.31
	t-bs	Topsoil basic saturation	4.12
	t.teb	Topsoil exchangeable base	6.48
	t.gravel	Topsoil gravel fraction (%vol.)	5.52

Species	Environment variables(Abbreviation)	Description	Contri
	t_ph-h2o	topsoil PH (h2o)	7.22

Table 2. The area and percentage of the different grades of habitat suitability under different climate scenarios

Species	Climate change scenario	Climate change scenario	Area/10 ³ km ² Unsuitable habitat	Area/10 ³ km ² Low suitable ha
<i>H. r. sinensis</i>	Current 2050s	Current	7272.79	1444.01
		SSP126	7055.04	1511.20
		SSP245	6900.33	1577.13
		SSP370	7035.31	1435.15
		SSP585	7112.00	1371.03
		Mean value	7025.67	1473.62
<i>H. r. turkestanica</i>	Current 2050s	Current	8200.46	1172.39
		SSP126	8016.65	1280.34
		SSP245	7727.44	1372.18
		SSP370	7820.87	1332.95
		SSP585	7878.76	1310.10
		Mean value	7860.93	1324.10

Table 3. Stable habitat percentage under different climate scenarios in the 2050s.

Species	Climate change scenario	Stable suitable habitat percentage (%)	Average percentage (%)
<i>H. r. sinensis</i>	SSP126-current	88.0	79.06
	SSP245-current	91.0	
	SSP370-current	88.1	
	RSSP585-current	89.4	
<i>H. r. turkestanica</i>	SSP126-current	76.0	76.90
	SSP245-current	81.8	
	SSP370-current	77.2	
	SSP585-current	80.2	

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Declaration of interests

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

AUTHOR CONTRIBUTIONS

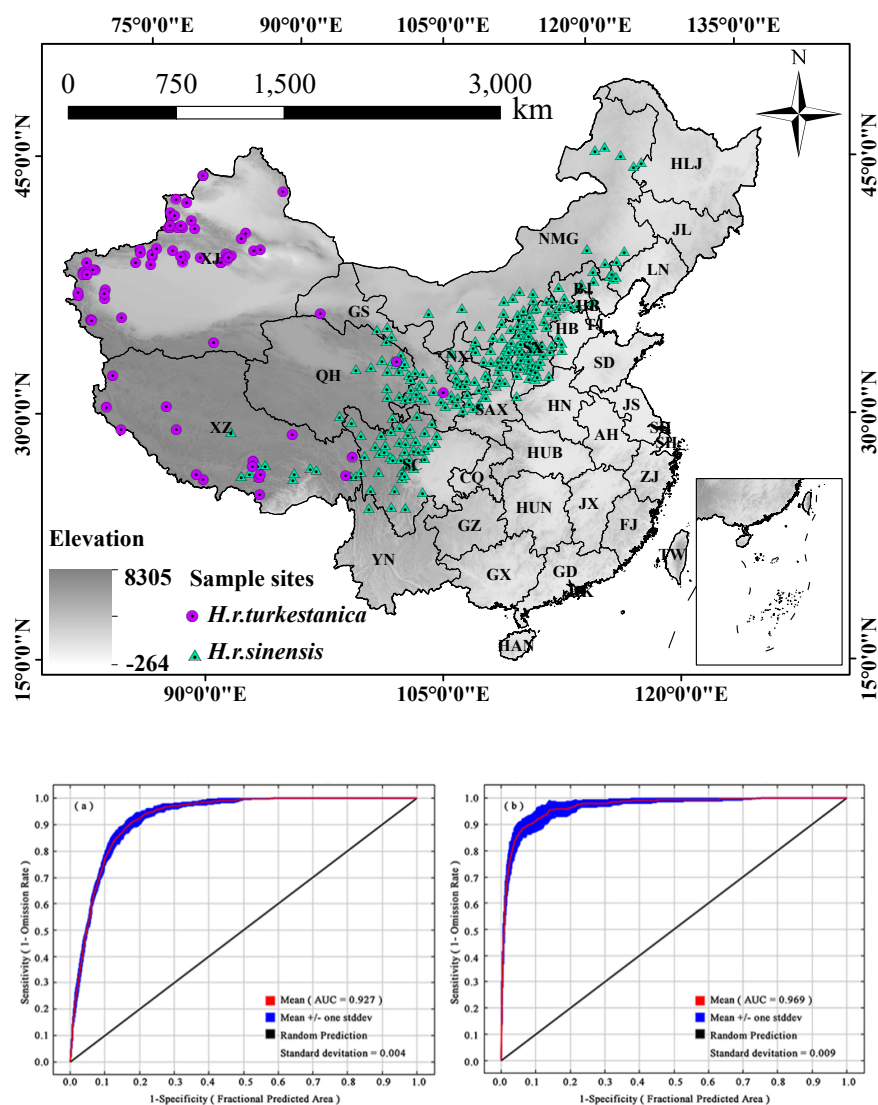
X-H H conceived the ideas, collected the data and write the manuscript; L Z collected the data; J-H S organized the manuscript; D-M Z, B J, and C-Y Z analyzed the data and results; C-L W, J Q, and X-L Z produced the figures and tables; all authors contributed critically to the drafts.

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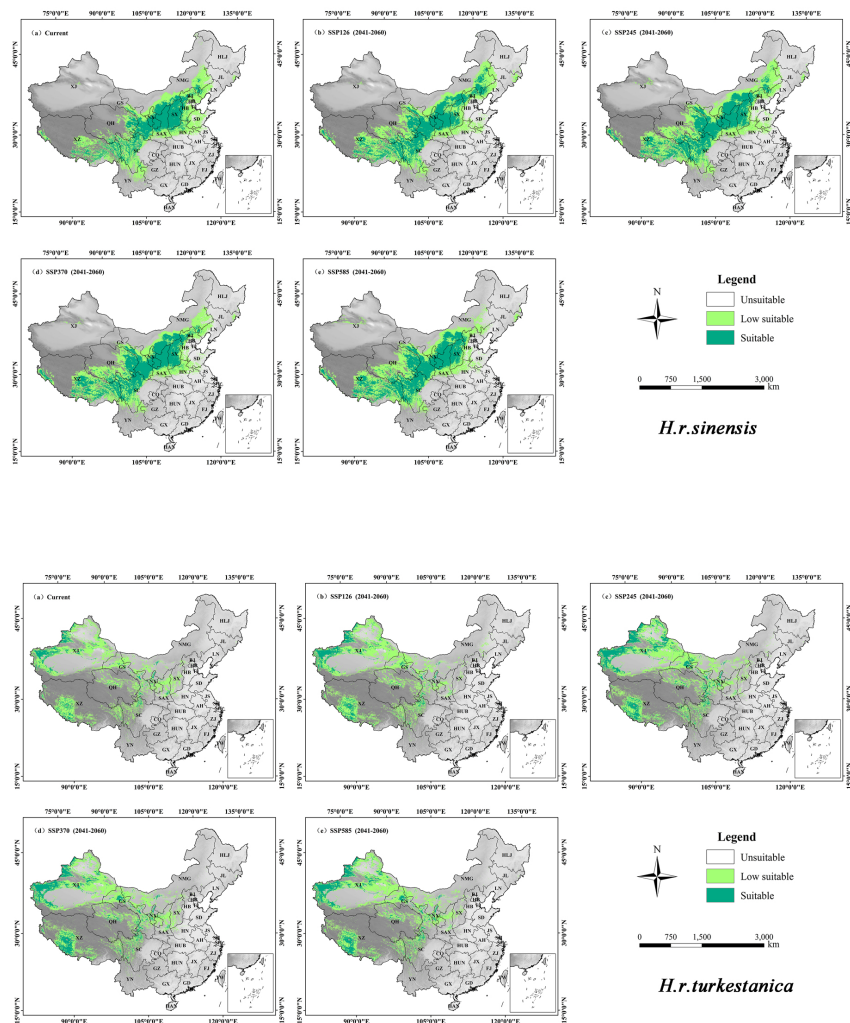
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