Postprint of the Potential Geographic Distribution of Three Cuscuta Species in China under Climate Change

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Abstract

All species in the Cuscuta genus are listed as quarantine plants due to their holoparasitic nature, and investigating the potential spatial distribution characteristics of Cuscuta species in China is of great importance for their prevention and control. This study selected three Cuscuta species—Cuscuta cupulata, Cuscuta campestris, and Cuscuta monogyna—as target species. Based on 932 existing geographic distribution records, 144 field survey records, and 20 environmental variables, we applied the Maximum Entropy Model and ArcGIS to predict their potential suitable habitat distributions under current and future (2041–2060, 2061–2080) SSP2-4.5 greenhouse gas emission concentration scenarios, and conducted overlay analysis between the suitable habitats of the three Cuscuta species under current climate scenarios and land use data. The results indicated that: (1) The Area Under the Receiver Operating Characteristic curve (AUC) values were all greater than 0.9, indicating high predictive accuracy. (2) The main environmental factors influencing the distribution of suitable habitats for the three Cuscuta species differed, but climatic factors were dominant in all cases, while the relative contribution of topographic factors was relatively small. (3) Under current climate scenarios, the suitable habitats of Cuscuta cupulata and Cuscuta monogyna were mainly distributed in northern China, whereas the suitable habitats of Cuscuta campestris were distributed not only in northern China but also extensively covered southeastern coastal areas. Moreover, all three Cuscuta species exhibited a trend of northward expansion in China in the future. (4) Most of the land within the suitable habitats of the three Cuscuta species has already been developed and utilized in the current period.

Full Text

Abstract

Cuscuta plants are classified as quarantine species due to their holoparasitic stem characteristics, and investigating their potential spatial distribution patterns in China is crucial for effective control. This study selected three Cuscuta species (*C. cupulata*, *C. campestris*, and *C. monogyna*) as research subjects. Based on 932 geographic distribution records, 144 field investigation records, and 20 environmental variables, we applied the maximum entropy model and ArcGIS to predict potential suitable area distributions under current and future climate scenarios (2041–2060, 2061–2080) using the SSP2-4.5 greenhouse gas emission pathway. We also overlaid the current climate scenario suitable areas with land use data. The results showed: (1) The area under the receiver operating characteristic curve (AUC) exceeded 0.9 for all species, indicating high prediction accuracy. (2) While the main environmental factors affecting the distribution of the three Cuscuta species varied, climate factors dominated in all cases, with topographic factors contributing relatively little. (3) Under current climate conditions, *C. cupulata* and *C. monogyna* suitable areas are concentrated in northern China, whereas *C. campestris* is distributed not only in the north but also extensively along the southeastern coast. All three species show a northward expansion trend in future scenarios. (4) Currently, most land suitable for these three Cuscuta species has already been developed.

Keywords: *Cuscuta*; MaxEnt model; potential suitable area; suitable area overlap; land use type

Introduction

Climate is one of the primary drivers of species range shifts, and global climate change is prompting range alterations in many plants [1]. Although invasive plants possess strong vitality and reproductive capacity, they are also highly sensitive to environmental changes [2], and their establishment and decline significantly impact local ecosystem structure and function. Therefore, studying potential suitable area distribution patterns of invasive plants under different climate change scenarios can help identify regions at risk of invasion, providing a theoretical basis for early warning and control measures.

Cuscuta, a representative genus in Convolvulaceae, is widely distributed in temperate and tropical regions. As typical holoparasitic plants, *Cuscuta* species have caused serious damage to agricultural ecosystems [3], using specialized haustoria to invade host vascular bundles and absorb water and nutrients. This parasitic behavior restricts host plant growth, potentially causing wilting and death, thereby severely affecting crop yield and quality [4]. Moreover, when *Cuscuta* populations become excessive, they threaten ecosystems [5] by reducing niches and resources provided by host plants to other organisms [6], affecting the growth of other plants and potentially causing local extinction of certain

species. Consequently, *Cuscuta* species have been listed as dangerous pests and quarantine weeds [7]. Current research on *Cuscuta* primarily focuses on morphological classification [8], allelopathy [9], and integrated control [10]; however, few studies have reported on the impacts of climate change on *Cuscuta* distribution patterns.

The MaxEnt model is an ecological niche theory model applicable to probability density assessment [11], using known species occurrence points and environmental data to simulate and predict the maximum ecological niche range a species could achieve under ideal, unconstrained dispersal conditions. This study employs the MaxEnt model to predict the current and future suitable areas of three *Cuscuta* species (*C. cupulata*, *C. campestris*, and *C. monogyna*) in China, and analyzes the dominant environmental factors affecting their potential distribution through environmental variable response curves, providing theoretical support for scientific prevention and control of *Cuscuta* invasions.

1.1 Species Distribution Data Sources

Distribution points for *C. cupulata*, *C. campestris*, and *C. monogyna* were obtained through field surveys conducted by our team in Xinjiang in recent years, yielding 144 distribution points. Additional data were collected from the Chinese Virtual Herbarium (https://www.cvh.ac.cn/), the Global Biodiversity Information Facility (https://gbif.org/), and published literature, totaling 932 national distribution points for the three *Cuscuta* species. To reduce sampling bias caused by clustering effects, we used ENMTools software to eliminate redundant data and avoid overfitting [12]. This software automatically matches the grid size of environmental variables and removes redundant data within the same grid cell, improving model prediction accuracy. After processing, effective distribution points were obtained for each species.

1.2 Environmental Variables

We obtained 20 climate factors and elevation data at 2.5 arc-minute spatial resolution from WorldClim (https://www.worldclim.org) , including current (1970–2000) and future (2041–2060, 2061–2080) environmental variables. Future climate data were selected from the CMIP6 (Coupled Model Intercomparison Project Phase 6) Shared Socioeconomic Pathway scenarios, specifically the SSP2-4.5 pathway under the CSM2-MR climate model. The CSM2-MR model effectively reproduces near-surface atmospheric mean temperatures [13], thus more accurately reflecting climate change trends.

To avoid model overfitting caused by multicollinearity, we used ENMTools software to analyze correlations among the 20 selected factors. When correlation coefficients $|r| > 0.8$ were found between factors, the variable with lower contribution was removed [14]. After screening, *C. cupulata*, *C. campestris*, and *C. monogyna* retained 6, 7, and 6 environmental variables, respectively .

1.3 MaxEnt Model Construction and Optimization

Different regularization multipliers and feature combinations in MaxEnt parameters can produce various models. To identify optimal parameter combinations and improve prediction accuracy [15], we ran the kuenm package in R, testing regularization multipliers from 0.1 to 4.0 (incrementing by 0.1) and combining them with five feature types (linear, quadratic, product, threshold, and hinge) in all permutations. We evaluated model fit and complexity using omission rates and Akaike Information Criterion to determine optimal parameter settings [16] .

Effective distribution points and screened environmental variables were imported into MaxEnt. For each species, 75% of distribution data were randomly selected for model training and the remaining 25% for testing. Optimal regularization multipliers and feature combinations were selected based on optimization results, with other settings kept at default and the model run 10 times.

1.4 Model Evaluation and Suitable Area Classification

Model prediction accuracy was assessed using the area under the receiver operating characteristic curve (AUC) [17]. AUC values closer to 1 indicate higher accuracy, with AUC > 0.9 representing excellent performance. The AUC values for *C. cupulata*, *C. campestris*, and *C. monogyna* all exceeded 0.9, confirming reliable predictions.

Using the reclassification tool in ArcGIS 10.4.1 and natural breaks classification, suitable areas were uniformly divided into four levels: high suitability [0.55–1.00], moderate suitability [0.25–0.55), low suitability [0.10–0.25), and unsuitable [0.00–0.10). Suitable area sizes were calculated for each climate scenario [18]. Raster calculator "multiply" and "add" functions were used to overlay current climate scenario suitable area raster layers (presence probability P $\geq$ 0.10) for the three *Cuscuta* species to identify co-occurring suitable regions.

2.1 Main Environmental Variables Affecting Potential Distribution of the Three Cuscuta Species

Contribution rates of climate variables to model construction [Figure 1: see original paper] revealed that climate factors dominate the potential distribution of all three *Cuscuta* species. The precipitation seasonality coefficient (Bio15) most strongly influenced *C. cupulata* and *C. monogyna*, while *C. campestris* was most affected by minimum temperature of the coldest month (Bio6). Elevation contributed minimally to potential distribution for all three species.

Species preferences for environmental factors are reflected in response curves. Presence probability > 0.5 indicates optimal growth conditions. Figure 2 shows that *C. cupulata* presence probability initially increases then decreases with rising mean temperature of the driest quarter, annual mean temperature, and

precipitation of the wettest month, while correlating negatively with precipitation seasonality. *C. campestris* presence probability increases with annual mean temperature, minimum temperature of the coldest month, temperature annual range, and mean temperature of the driest quarter, reaching high and stable levels when annual mean temperature > 17.67°C, minimum temperature of coldest month > 25.75°C, and mean temperature of driest quarter > 24.93°C. *C. monogyna* presence probability decreases with increasing precipitation seasonality, precipitation of the wettest month, and mean diurnal temperature range, while increasing with temperature seasonality.

2.2 Potential Distribution of Three Cuscuta Species in China Under Current Climate Scenarios

MaxEnt predictions [Figure 3: see original paper] indicate that under current climate conditions, *C. cupulata* has a total suitable area of 588.54$×10^{4}$ km^2 in China, accounting for approximately 61.09% of China' s land area. It is mainly distributed in northwestern, northern, and northeastern China, with parts of southwestern China. High-suitability areas concentrate in northern Xinjiang, northwestern southern Xinjiang, northwestern Gansu, and parts of southern Tibet. Moderate-suitability areas, besides surrounding high-suitability zones, are mainly found in Gansu, Ningxia, Shaanxi, Shanxi, Inner Mongolia, Heilongjiang, Jilin, and Liaoning, with local distributions in Qinghai, Sichuan, Yunnan, Shandong, Hebei, and Henan.

Cuscuta campestris has a total suitable area of 117.45$×10^{4}$ km^2, representing about 12.19% of China' s land area. Its high-suitability areas are primarily in southeastern coastal regions and parts of the Tianshan Mountains in Xinjiang. Moderate-suitability areas, besides surrounding high-suitability zones, are mostly in Guangxi and Fujian, with smaller portions in Jiangxi, Tibet, and Inner Mongolia.

Cuscuta monogyna has a total suitable area of 258.52$×10^{4}$ km^2, accounting for approximately 26.83% of China' s land area. It is concentrated in northwestern China with scattered distributions in northeastern, northern, central, and southwestern China. High-suitability areas are mainly in northern and western Xinjiang and parts of central Tibet. Moderate-suitability areas, besides surrounding high-suitability zones, are concentrated at the junctions of Gansu, Shaanxi, Shanxi, Hubei, and Sichuan, with scattered distributions in Inner Mongolia, Qinghai, Guizhou, and Chongqing.

Overlay analysis revealed co-occurring suitable areas for the three *Cuscuta* species under current climate conditions [Figure 3: see original paper]. The total overlapped suitable area is 673.44$×10^{4}$ km^2, representing about 70.15% of China' s area. Every province contains at least one *Cuscuta* species' suitable area, with co-occurring regions concentrated in northwestern China (most of Xinjiang and parts of Inner Mongolia and Gansu).

2.3 Potential Distribution of Three Cuscuta Species in China Under Future Climate Scenarios

Predictions for future climate scenarios and area changes are shown in [Figure 4: see original paper] and [Figure 5: see original paper]. Compared with current conditions, *C. cupulata*' s total suitable area decreases to varying degrees in both future periods. *Cuscuta campestris* shows increased total suitable area in both future periods. *Cuscuta monogyna* exhibits an initial increase followed by a decrease. However, high-suitability areas for all three species increase to varying degrees in all future periods compared with current conditions.

2.4 Centroid Migration of Potential Distribution Areas Under Future Climate Scenarios

Figure 6 shows that *C. cupulata*' s suitable area centroid is located in northeastern Gansu, showing a consistent northwestward migration trend. *Cuscuta campestris* centroids are mainly in northern Sichuan, with substantial movement first northeastward then northwestward. *Cuscuta monogyna* centroids are primarily in northern Gansu, with future centroids showing large east-west migration but remaining north of the current centroid.

Discussion

Analysis of land use types in current climate scenario suitable areas for the three *Cuscuta* species reveals that most suitable land has been developed. For *C. cupulata*, undeveloped land in potential suitable areas is 154.78$\times$10^{4}$ km^2, representing 26.30% of its suitable area. For *C. campestris*, undeveloped land is 23.75$\times$10^{4}$ km^2 (20.22% of suitable area). For *C. monogyna*, undeveloped land is 91.79$\times$10^{4}$ km^2 (35.10% of suitable area) [Figure 7: see original paper] .

Invasive plant spread severely impacts native biodiversity and ecosystems. *Cuscuta* species are highly invasive, with the entire genus listed as quarantine weeds. Their high seed production and twining stem parasitism give them competitive advantages in natural environments. This study used MaxEnt modeling to predict potential distributions of *C. cupulata*, *C. campestris*, and *C. monogyna* across China, with prediction accuracies exceeding 0.9, confirming reliable results.

Cuscuta species have broad suitable ranges, with every Chinese province containing potential suitable areas for at least one species, though each species shows regional specificity [19]. Our results indicate that environmental factors influencing the potential distributions of *C. cupulata*, *C. campestris*, and *C. monogyna* differ, with varying niche parameters for dominant factors, potentially explaining the genus' s wide distribution. Climate factors dominate *Cuscuta* distribution, with elevation contributing minimally, consistent with Ren [20] who identified climate as the primary limiting factor.

Cuscuta campestris is native to North America and was first reported as an invasive plant in Fujian in 2014 [21], with numerous distribution points now in Taiwan and Xinjiang. Taiwan' s coldest month mean temperature ranges from 10.38–23.11°C, remaining summer-like year-round and providing suitable conditions for *C. campestris* germination. The abundance of Taiwan distribution points indicates *C. campestris* has become rampant there. *Cuscuta cupulata* originates from North Africa, southwestern Asia, and southern Europe [22]. Its simulated suitable areas differ substantially from *C. campestris*, likely due to species-specific biological characteristics. Ren [20] predicted suitable areas for three other *Cuscuta* species, also showing significant differences, demonstrating the genus' s strong environmental adaptability. Although *C. monogyna* is not listed as invasive, its current global distribution resembles that of invasive *C. cupulata* [24,27], but with notably fewer moderate- and low-suitability areas, possibly because *C. monogyna* is more precipitation-sensitive. Esmall [28] reported that *C. monogyna* seeds struggle to germinate in high-moisture soils. Both invasive *Cuscuta* species show promoted seed germination under low-temperature stress [29,30]. Xinjiang' s early snowfall, long snow cover period, hot summers, abundant snowmelt water, and vast territory offer considerable expansion potential for *Cuscuta* species.

Under ongoing global warming, most flora and fauna show poleward migration trends [31], though direction and magnitude vary due to species differences and environmental complexity [32]. This study found that with future warming and wetting trends, high-suitability areas for all three *Cuscuta* species increase, with total suitable areas expanding northward into higher latitudes. Jilin, Inner Mongolia, Ningxia, Shaanxi, Shandong, Jiangsu, and Guizhou currently lack distribution records for these three species but contain potential suitable areas for at least two species, with Inner Mongolia containing potential suitable areas for all three. Vigilance is needed against *Cuscuta* spread to new regions. All three species maintain high-suitability areas in Xinjiang. With approximately 200 *Cuscuta* species globally and 11 in China [33], Xinjiang' s role as a major economic and cultural exchange corridor with numerous ports necessitates heightened attention to quarantine weed introduction and spread. Overlay analysis of current climate scenario suitable areas with land use data shows most land is already developed. Relevant regions should prioritize preventing negative ecosystem impacts from *Cuscuta* invasion, exercising caution when developing unused land to enable early prevention and control before invasions become established.

Conclusion

Based on MaxEnt modeling and species distribution data, under current climate scenarios, high-suitability areas for *C. cupulata* and *C. monogyna* concentrate in Xinjiang, while *C. campestris* has fewer high-suitability areas, mainly in Taiwan, northern Hainan, southern Guangdong coast, and parts of Xinjiang. Every Chinese province contains at least one *Cuscuta* species' suitable area. Most suitable

land for the three *Cuscuta* species has been developed, making these vegetation zones vulnerable. Precipitation and temperature are the main drivers constraining current and future *Cuscuta* distributions, with elevation contributing relatively little. Under future climate scenarios, high-suitability areas for all three species increase to varying degrees, with total suitable area centroids shifting northward. In summary, *Cuscuta* species benefit from future warming scenarios, with potential high-suitability areas further increasing. Inner Mongolia, Jilin, Ningxia, Shaanxi, Shandong, Jiangsu, and Guizhou currently lack distributions but contain potential suitable areas, requiring vigilance against invasion. Xinjiang' s climate conditions align with *Cuscuta* ecological habits, necessitating strengthened prevention and control. These results provide important theoretical support for monitoring, early warning, and scientific management of the three *Cuscuta* species.

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Note: Figure translations are in progress. See original paper for figures.