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Original Research

Analysis of Interrelationship between Shrubs and Herbs Using Maximum Entropy

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Abstract

A scientifically robust classification of biogeographical regions, along with research on their interdependencies, is essential for enhancing our understanding of biodiversity dynamics, ecological conservation, and natural resource management. In this study, we partitioned the biogeographic regions of Inner Mongolia's desert-steppe ecotone using the Maximum Entropy (MaxEnt) model. The results indicated that the study area could be divided into shrub and herb regions. The model effectively simulated the potential distributions, yielding an area under the curve >0.8. The contribution of biological interactions to the shrub and herb regions was relatively high, reaching 34.8% for both shrubs and herbs. The two regions primarily compete for precipitation during the wettest month, with optimal precipitation ranges of 10.12-65.01 mm for shrubs and 26.90-86.90 mm for herbs. When biological effects were incorporated into the model, the distribution areas of both regions decreased, although their average suitability remained stable. This study quantitatively validates the significance of biological factors through modeling and provides a data-driven foundation for the development of regional conservation strategies.

Keywords: biogeographic regions, limiting factor, distribution area, MaxEnt model, suitable habitat

Introduction

Geographically distinct assemblages of species and communities are known as biogeographic regions [1, 2]. Studying these regions and exploring their interrelationships can provide a deeper understanding of biodiversity distribution, which is highly significant in the fields of ecology, evolutionary biology, and conservation [3].

Recent research on biogeographic regions has primarily focused on the application of various regionalization methods. Gross et al. (2025) [4] delineated biogeographic regions of butterflies by leveraging phylogenetic dissimilarity and identifying 19 distinct phylogenetically defined nested regions. Gao and Kupfer (2018) [5] conducted a biogeographic regionalization of mammalian species distribution in Angola using both non-spatial and spatial clustering methods. Boone (2024) [6] defined hierarchical biophysical regions based on plant productivity and phenology by clustering global 0.083° normalized difference vegetation indices over ten years. Another

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area of research involves utilizing ecological criteria to identify regions for biodiversity conservation, enhancing the understanding of biogeographic regionalization, and establishing principles for area-based biodiversity conservation. Asaad et al. (2017) [7] selected eight criteria commonly used to identify areas for biodiversity conservation from a set of ecological and biological standards. Morrone (2018) [2] proposed a general protocol for conducting biogeographic regionalization. Riva et al. (2024) [8] argued that there are three essential principles of area-based biodiversity conservation. Although numerous studies have been conducted to delineate biogeographic regions, there is still no specific method to accurately divide the geographical regions of shrub and herb areas in the Inner Mongolia desert-steppe ecotone.

Shrubs and herbs are the two dominant plant types in arid and semi-arid regions [9, 10], forming grassland and shrubland ecosystems. The distribution of shrubs and herbs is influenced by both negative and positive factors, such as competition and facilitation, and varies according to location and other environmental conditions [11, 12]. (i) Shrubs promote herb growth. Xie et al. (2023) [13] found that shrubs facilitate herb communities in deserts by modifying the soil properties in Alashanzuo, which is located on the Inner Mongolian Plateau in China. El-Bana et al. (2002) [14] studied the effects of widely spaced nebkhas of the *Retama raetam* shrub on their microenvironment and the associated herb vegetation along the Mediterranean coast of the Sinai Peninsula, Egypt. They found that shrubs and other deep-rooted plants might enhance nutrient availability in grasslands by transferring nutrients from deeper soils to the soil surface through leaf litter. (ii) Shrubs and herbs have a competitive relationship [15]. Sala et al. (1989) [16] conducted an experiment in the Patagonian steppe of southern South America, where grasses and shrubs were selectively removed. Their results indicated that the removal of shrubs did not alter grass production, but the removal of grasses resulted in a small increase in shrub production. This is because grasses and shrubs primarily utilize different resources. McCarron and Knapp (2001) [17] and Rodríguez et al. (2007) [18] found that, in arid and semi-arid ecosystems, shrubs exploit both shallow and deep soil waters, thereby competing to some extent with grasses. In the *Calluna*-dominated heaths of the Netherlands [19], shrubs are confined to nutrient-poor sites and are seemingly outcompeted by grasses under nutrient-rich conditions. (iii) The effects of shrubs on herbs vary among life stages and plant species [20]. Pierce et al. (2019) [21] experimentally manipulated grass-on-shrub interactions during the early and late stages of grassland-shrubland state transitions in semi-arid and sub-humid savannas. They found that, in the early stages of shrub invasion, competition from herbs reduced shrub growth. Conversely, in the later stages of the grassland to shrubland transition, competition among the shrubs did not impede the rate of shrub expansion. Liu et al. (2023) [22] observed that plant communities transitioned from perennial herbs to shrub-herb communities and ultimately to shrub communities, with *Vitex negundo* var. *heterophylla* dominating the succession of shrub-herb communities in the hilly region of the Taihang Mountain. Although numerous studies have investigated the relationship between shrubs and herbs, they are often limited to specific locations and lack analysis of the spatial distribution relationship between shrubs and herbs at a regional scale.

Species distribution models identify the ecological niches of species and the environmental conditions required to fulfill those niches [23, 24]. The MaxEnt model is the most widely used species distribution model because it has no strict requirements for sample size and is easy to explain from an ecological perspective [25, 26]. The model is widely used to simulate species distribution and identify suitable habitats by establishing the relationship between species and their environment [27-29]. However, this distribution model relies on environmental variables for prediction and ignores other critical determinants that affect species distribution. Among these determinants, biological interactions are particularly important.

The desert-steppe ecotone in Inner Mongolia is highly sensitive to climate change [30]. Shrub expansion and concomitant grassland degradation represent a critical threat to ecosystem sustainability in the ecotone. Owing to climate change and human activities, natural vegetation types have undergone substantial changes. Therefore, based on the ecological geographical zoning, this study combines the actual distribution of plant longitude and latitude data within the ecological zoning with regional environmental factors to reconstruct the relationship between the environment and vegetation. The main contents include environmental variable screening, model selection, parameter configuration, threshold determination, and result assessment.

The specific objectives were as follows: (i) to identify the limiting factors of biogeographic regions, (ii) to determine the extent of the distribution of current biogeographic regions, and (iii) to map the spatial distribution of these biogeographic regions.

Materials and Methods

Study Area

The study area is situated in the ecotone of the desert-steppe in Inner Mongolia, China (105°9’-112°1’E, 37°28’-43°48’N, 876-1,823 m above sea level; Fig. 1). It spans an east-west length of approximately 1,110 km and a north-south distance of 448 km. From west to east, the mean annual temperature ranges from 8.8 to 5.0ºC, while annual precipitation varies from 68 to 299 mm, with 60-75% of the precipitation occurring between June and August (http://www.worldclim.org/).

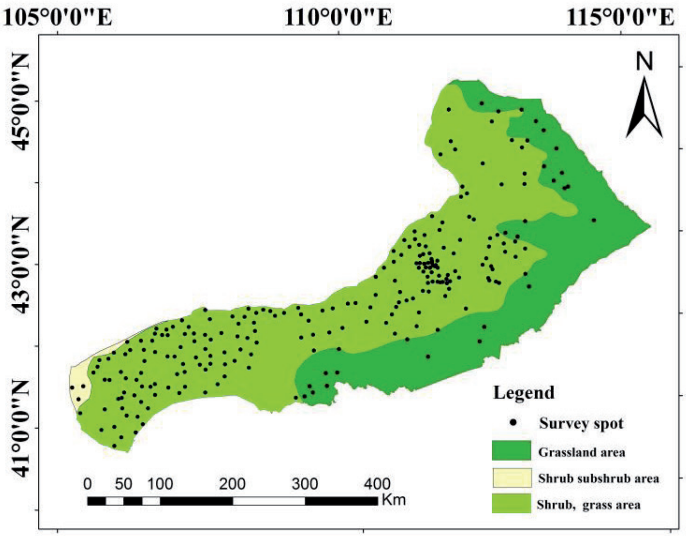

Fig. 1. The location of the desert-steppe ecotone and sampling points.

This precipitation gradient significantly influences the distribution, structure, and function of vegetation within the ecotone. Shrub deserts are predominant in the western region, whereas grasslands dominate the eastern region. The central area is characterized by a mix of steppe desert and steep desert landscapes.

Experimental Design

Data Collection

Based on the 1:1,000,000 vegetation map of China (https://www.plantplus.cn/dsite/zhibei/b12.html) and the vegetation type map derived from MODIS 250×250 m data (https://ladsweb.modaps.eosdis.nasa.gov/), survey sites for the primary plant communities in this region were systematically selected following a 10×10 km grid principle. A total of 265 community sampling sites were established (Fig. 1).

Field surveys and sample collection were conducted between July and August 2020. At each site, a large quadrat measuring 100×100 m was established, along with five sub-quadrats (10×10 m) and nine sub-quadrats (1×1 m) to survey the shrub and herb layers. The plant species, coverage, and height of each species within each quadrat were then recorded. A total of 62 shrub species and 182 herb species were identified in the study area. The classification of the vegetation community was based on the dominant species, which were determined based on their importance.

The species importance value at each site was calculated using Equations (1-4).

$$RI = (CR + HR + DR)/3 \tag{1}$$

$$DR = \text{The abundance of a species /sum of the abundance of all species} \tag{2}$$

$$CR = \text{The coverage of a species /sum of the coverage of all species} \tag{3}$$

$$HR = \text{The average height of a species/ the average height of all species} \tag{4}$$

where RI, CR, HR, and DR are the relative importance value, relative coverage, relative height, and relative density, respectively.

Biogeographic Regions Division and Occurrence Records

Based on the dominant species within each plant community, the main shrub species are *Zygophyllum xanthoxylum*, *Nitraria tangutorum*, *Artemisia ordosica*, *Reaumuria songarica*, *Caragana tibetica*, *Potaninia mongolica*, *Caragana korshinskii*, *Nitraria sphaerocarpa*, *Haloxylon ammodendron*, *Krascheninnikovia ceratoides*, *Kalidium gracile*, and *Caroxylon passerinum*. The herb species mainly include *Stipa tianschanica* var. *gobica*, *Stipa breviflora*, and *Allium polyrhizum*. The study area was categorized into shrub (shrub desert, steppe desert, and desert) and herb regions (steppe desert, desert, and grassland). The longitudinal and latitudinal data of the dominant species in each region were compiled, and the distribution of shrubs and herbs was simulated.

In addition to the data collected at each site, supplementary species information was obtained by consulting the Chinese Virtual Herbarium (https://www.cvh.ac.cn/index.php) and the Global Biodiversity Information Facility (GBIF; http://www.gbif.org) to enhance the growth data for each region. Duplicate and erroneous entries were eliminated, and the refined data were used to develop the MaxEnt model.

Environmental Variables and Correlation Analysis

The environmental input data for MaxEnt included a digital elevation model (DEM) of the study area, along with a suite of spatially explicit climate and soil data. DEM and climate data covering the period from the 1970s to the 2000s were obtained from the WorldClim database (http://www.worldclim.org/). Topographical variables, such as slope and aspect, were derived from the DEM using ArcGIS 10.6 (Environmental Systems Research Institute; http://www.esri.com/). Soil data were sourced from the Harmonized World Soil Database (http://www.fao.org/faostat/en/#data).

To minimize redundancy among environmental variables, SPSS version 25.0 (IBM Inc., Chicago, IL, USA) was used to perform a factor correlation analysis. If the correlation coefficient between the two variables exceeded 0.8, the variable with the greatest influence was selected. The environmental factors considered in this study are listed in Table 1.

MaxEnt Model

MaxEnt models species distributions and environmental niches using presence-only data based on the principle of maximum entropy [31]. MaxEnt version 3.4.1 was utilized to project the potentially suitable environmental distribution of shrub and herb regions, and it was downloaded from https://biodiversityinformatics.amnh.org/open_source/maxent/. In the model, the training dataset was allocated 75% of the data, whereas the validation dataset comprised 25% of the data to enhance the accuracy of the analysis. This process was repeated ten times, and the average results were analyzed to minimize errors.

This study first ran the MaxEnt model using environmental factors only to obtain initial suitability distribution maps for both shrubs and herbs. The initial suitability map of the herb layer was then incorporated as a new ‘environmental layer’ into the second model run for shrubs, and vice versa. The Jackknife method was used to examine the primary environmental factors affecting vegetation type distribution. The cumulative contribution of the selected environmental factors to the spatial distribution of each vegetation type exceeded 80%.

The prediction accuracy of the model was assessed using the area under the receiver operating characteristic curve (AUC). The AUC values ranged from 0 to 1, with higher values indicating superior model performance. An AUC of <0.5 suggests that the predictive ability of the model is inferior to that of a random model. Model performance is categorized as follows: failure (0.5-0.6), poor (0.6-0.7), fair (0.7-0.8), good (0.8-0.9), and excellent (0.9-1.0).

Extraction of Species Suitability and Calculation of Suitable Area

MaxEnt minimizes the discrepancy between the predicted and observed distributions by establishing a threshold known as the Maximum Test Sensitivity plus Specificity Logistic Threshold (MTSPS) for each plant species [32, 33]. The Habitat Suitability Index (HSI) was calculated for each grid element within the study area. If the HSI exceeded the MTSPS, the species was considered suitable for thriving; otherwise, it was considered to be unsuitable.

HSI values were extracted from two biological regions. Suitable areas were determined based on the number of pixels that occupied each region. All processes were conducted using ArcGIS 10.6 (Environmental Systems Research Institute; http://www.esri.com/).

Results

MaxEnt Model Evaluation

Model accuracy was assessed using the Area Under the Curve (AUC) statistic, a widely adopted measure in ecological niche modeling for evaluating the discriminatory power of a model. The AUC values for the shrub and herb regions were both >0.80 (Table 2). These results indicate that the model predictions are reliable and can be used for further analysis. The logistic threshold established by the model was used to differentiate between suitable and unsuitable areas, and the specific thresholds for each biogeographic region are presented in Table 2.

Effects of Environmental Factors on Biogeographic Regional Distribution

The primary environmental factor influencing the regional distribution of shrubs was Bio 13, which accounted for a contribution rate of 80.0%. The environmental factors affecting the distribution of herbs included Bio 13, Bio 14, S_CACO3, S_CLAY, Bio 3, and Bio 6. Together, these six factors had a cumulative contribution rate of 84.1% (Table 3).

After incorporating herb suitability into the analysis of shrub distribution, this factor emerged as a dominant one with an extremely high contribution rate, alongside Bio13. Together, these factors accounted for 85.5% of the cumulative contribution. Conversely, when shrub suitability was included in the analysis of herb distribution, it also became a dominant factor. The cumulative contribution of shrub suitability, Bio14, and Bio6 reached 82.0% (Table 3). This indicates that shrub habitat suitability significantly influences herb distribution, and vice versa. Furthermore, after accounting for biological interactions, the response curves of the factors to biogeographical distribution

Table 1. Codes and details of the environmental factors.

Category	Paraphrase	Factor	Unit
Climate	Mean annual temperature	Bio 1	ºC
-	Mean Diurnal Range	Bio 2	ºC
-	Isothermality	Bio 3	-
-	SD of Temperature Seasonality	Bio 4	-
-	Max temperature of warmest month	Bio 5	ºC
-	Min temperature of coldest month	Bio 6	ºC
-	Temperature Annual Range	Bio 7	ºC
-	Mean temperature of wettest quarter	Bio 8	ºC
-	Mean temperature of driest quarter	Bio 9	ºC
-	Mean temperature of warmest quarter	Bio 10	ºC
-	Mean temperature of coldest quarter	Bio 11	ºC
-	Annual precipitation	Bio 12	mm
-	Precipitation of wettest month	Bio 13	mm
-	Precipitation of driest month	Bio 14	mm
-	Precipitation Seasonality (Coefficient of Variation)	Bio 15	mm
-	Precipitation of wettest quarter	Bio 16	mm
-	Precipitation of driest quarter	Bio 17	mm
-	Precipitation of warmest quarter	Bio 18	mm
-	Precipitation of coldest quarter	Bio 19	mm
Topography	Aspect	Aspect	rad
-	Slope	Slope	°
-	Elevation	Elev	m
Soil	Topsoil/Subsoil Gravel Content	T/S_Gravel	%
-	Topsoil/Subsoil Sand Fraction	T/S_Sand	%
-	Topsoil/Subsoil Silt Fraction	T/S_Silt	%
-	Topsoil/Subsoil Clay Fraction	T/S_Clay	%
-	Topsoil/Subsoil USDA Texture Classification	T/S_USDA_TEX	-
-	Topsoil/Subsoil Reference Bulk Density	T/S_REF_BULK	kg/dm^3
-	Topsoil/Subsoil Organic Carbon	T/S_OC	mg/kg
-	Topsoil/Subsoil pH (H_2O)	T/S_Ph_H_2O	−log(H+)
-	Topsoil/Subsoil CEC (clay)	T/S_CEC_CLAY	-
-	Topsoil/Subsoil CEC (soil)	T/S_CEC_SOIL	-
-	Topsoil/Subsoil Base Saturation	T/S_BS	-
-	Topsoil/Subsoil TEB	T/S_TEB	-
-	Topsoil/Subsoil Calcium Carbonate	T/S_$CACO_3$	%
-	Topsoil/Subsoil Gypsum	T/S_$CASO_4$	%
-	Topsoil/Subsoil Sodicity (ESP)	T/S_ESP	%
-	Topsoil/Subsoil Salinity (Elco)	T/S_ECE	mS/m

Table 2. AUCs and the logistic threshold for shrub and herb regions.

Type	Abiotic Factors only		Abiotic Factors + Biological Factors	
	AUC	Logistic Threshold	AUC	Logistic Threshold
Shrub region	0.88	0.21	0.88	0.22
Herb region	0.82	0.37	0.82	0.36

Table 3. The main environmental factors affecting the distribution of shrub and herb regions and their contribution rates.

Type		Variable (%)					
Abiotic Factor	Shrub region	Bio13 (80.0)	-	-	-	-	-
-	Herb region	Bio13 (38.4)	Bio14 (11.7)	S_CACO_3 (11.4)	S_CLAY (10.0)	Bio3 (7.4)	Bio 6 (5.2)
Abiotic Factors + Biological Factors	Shrub region	Bio13 (73.9)	Herb Suitable (11.6)	-	-	-	-
-	Herb region	Shrub Suitable (34.8)	Bio13 (32.1)	Bio14 (10.0)	Bio 6 (5.1)	-	-

showed no significant changes (Figs 2-3). Therefore, the biological interaction effects observed in this study primarily manifest as a redistribution of contribution rates among the key environmental factors.

Relationship between Ecological Factors in Two Biogeographic Regions

The two biogeographic regions overlapped only in Bio 13 (Table 4). The range of Bio13 within the shrub region spanned from 10.12 to 65.01 mm, whereas the range within the herb region extended from 26.9 to 86.9 mm. Under the influence of this specific factor, the ecological niche in the herb region was broader than that in the shrub region, leading to resource competition between the two within the range of 26.9 to 65.01 mm (Table 4). Furthermore, the remaining environmental factors influencing the distribution of these biogeographic regions were distinct, with each factor affecting the distribution patterns.

There was no significant change in the utilization range of ecological factors when the biological region was simulated using only environmental factors or when biological effects were included.

Influence of Biological Factors on Suitable Areas of Bioregions

The distribution areas of the biogeographic regions before and after the incorporation of the biological factors are shown in Fig. 4. When only environmental factors were considered, the suitable distribution areas for shrubs and herbs in Inner Mongolia were 3.41×10^5 km^2, whereas that for herbs was 2.03×10^5 km^2. The overlapping area between the two was 1.14×10^5 km^2 (Table 5). When the suitability of herbs was considered to assess their influence on the distribution of the shrub region, the area of the shrub region decreased by 0.01×10^5 km^2 compared with the previous scenario. Under the influence of shrub suitability, the area of the herb region decreased by 0.28×10^5 km^2, resulting in an overlapping area of 1.09×10^5 km^2. This evidence indicates a competitive relationship between the shrub and herb regions.

Effects of Biological Actions on Habitat Suitability

When comparing the regional suitability of shrubs and herbs, the mean suitability for shrubs was 0.42 (range: 0.01-0.85), whereas for herbs, it was 0.39 (range: 0.01-0.87) under environmental factors (Fig. 5). After incorporating biological factors that influence the distribution of these biological regions, the mean suitability value for the shrub region remained at 0.42 (range: 0.01-0.87), and the mean suitability value for the herb region remained at 0.39 (range: 0.01-0.86). However, biological factors altered the maximum values of the biological regions. The inclusion of suitable layers for shrubs decreased the regional suitability of herbs, whereas the addition of suitable layers enhanced the regional suitability of shrubs.

Discussion

Biological and Abiotic Factors Determine Distribution of Biogeographic Regions

The primary environmental factor influencing the distribution of shrub and herb regions was Bio13 (Table 3), which indicates that precipitation plays a crucial role

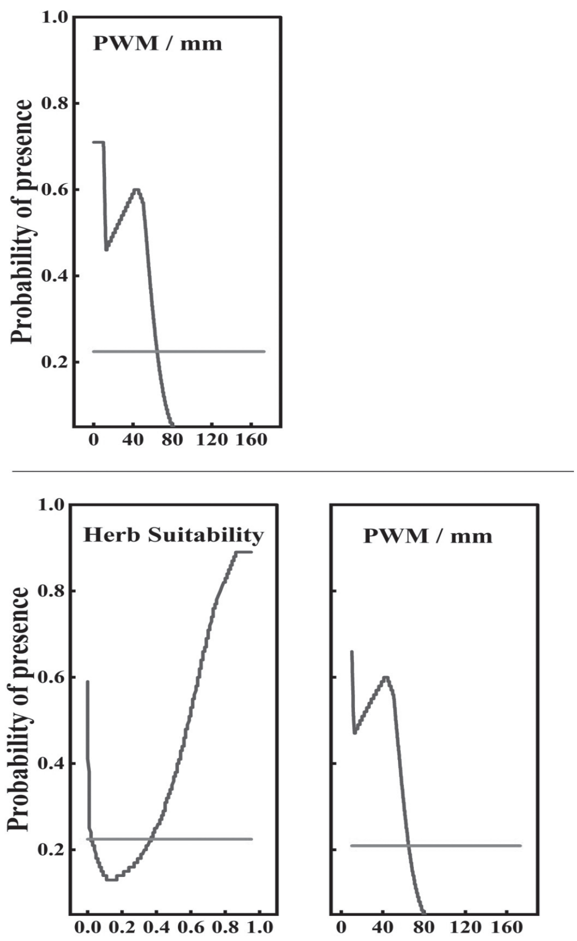

Fig. 2. The main factors affecting the shrub region.

in shaping the distribution of these regions within the ecotone of the desert-steppe. Water is a vital resource that limits plant growth [34].

When biological factors were considered as environmental influences on the distribution of biogeographic regions, their contribution rates were the highest (Table 3; Figs 2-3). This finding aligns with the research conducted by Staniczenko et al. (2017) [35], Paquette et al. (2021) [36], and Galiana et al. (2023) [37], which underscores the significant role of biotic interactions in defining the extent of species' ranges. However, our study focused on validating a model that assessed the impact of biological factors on the distribution of bioregions.

The lack of significant change in the environmental response curves after incorporating biological interactions suggests that the tolerable environmental range for the species remains stable. The changes in suitable distribution areas represent the species' realized niche. This indicates that while interactions between shrubs and herbs do not affect a species' ability to survive at a given location, they determine its success in establishing itself when facing competition. Therefore, in the context of climate change, a species' migration potential is likely primarily determined by its fundamental niche, but the final composition of the community will be shaped by interspecific interactions. Predicting community dynamics thus requires consideration of both environmental drivers and biological interactions.

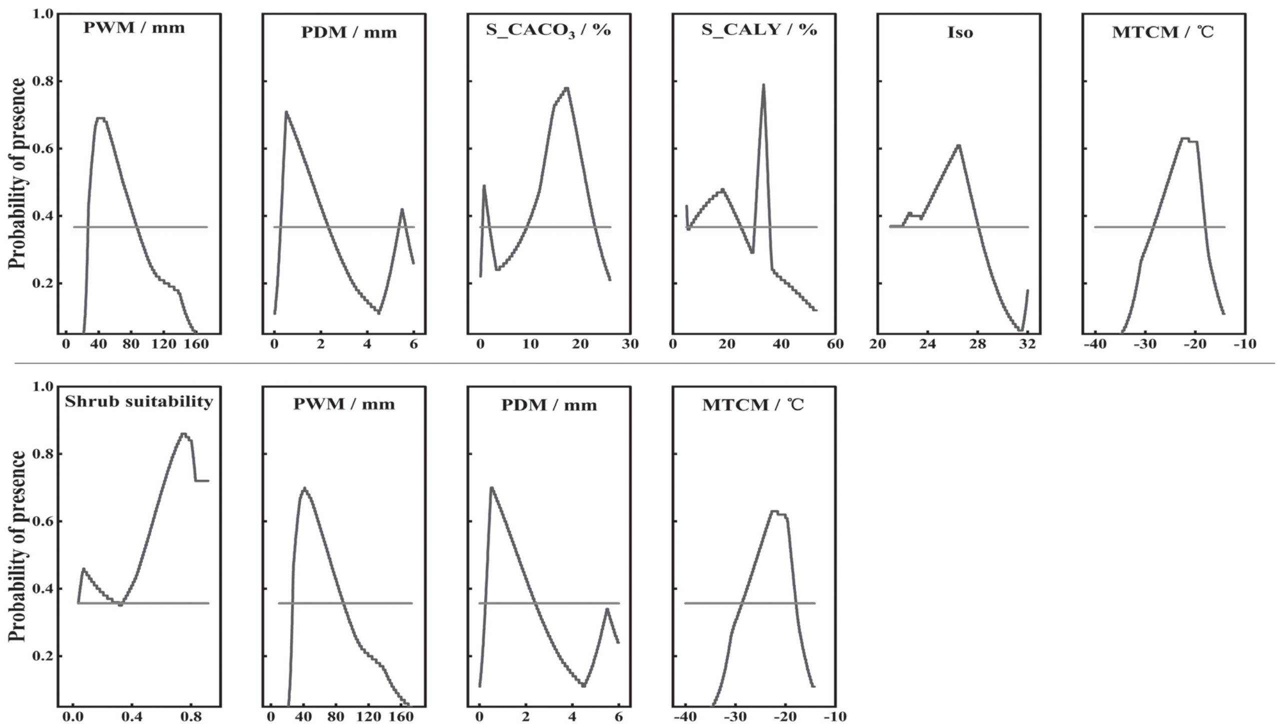

Fig. 3. The main factors affecting the herb region.

Table 4. The amplitude of major environmental factors affecting the distribution of shrub and herb regions.

Type		Bio13 (mm)	Bio14 (mm)	Bio6 (°C)	Bio3	S_CACO$_3$ (%)	S_CLAY (%)	Herb Suitable	Shrub Suitable
Abiotic Factor	Shrub region	10.12-65.01	-	-	-	-	-	-	-
-	Herb region	26.9-86.9	0.27-2.32	-3.75-(-2.71)	21.00-28.04	0.43-1.83, 9.28-22.92	5.04-25.08, 30.21-35.74	-	-
Abiotic Factors + Biological Factors	Shrub region	0.09-64.29	-	-	-	-	-	0-0.2, 0.37-0.95	-
-	Herb region	26.56-89.15	0.26-2.40	-39.99-(-14.2)	-	-	-	-	0.04-0.92

Utilization of Precipitation in Shrub and Herb Regions Is different

Both shrub and herb regions compete for precipitation resources, with and without biological activity (Table 4). Competition for water among plants is particularly intense in arid and semi-arid environments [38, 39]. Therefore, competitive effects must be assessed in similar environments. The shrub and herb regions examined in our study were both located in a desert-steppe ecotone, which enhances the reliability of our conclusions.

The drought tolerance of the shrub region was greater than that of the herb region (Table 4). The herb region exhibited a wide range of adaptability to varying precipitation levels. Because shrubs possess significantly deeper root systems than herb plants [40], they are more proficient at exploiting surface resources [41]. Under arid conditions, shrubs are more effective than herb plants at utilizing groundwater. Consequently, shrubs can mitigate the effects of soil moisture depletion by accessing both water sources [42].

Competition between Shrubs and Herbs

When biological factors were considered to assess their influence on the distribution, the distribution areas of both biogeographic regions decreased (Table 4; Fig. 4). The herb region competed with the shrub region in terms of spatial distribution, and the shrub region had a more significant impact on the herb region. Consequently, after herb degradation, shrubs may proliferate in large numbers, resulting in grassland–scrub formation [43].

Shrubs are often considered undesirable in grasslands and are typically removed during management, suggesting that they negatively affect grass growth. Herb plants are more prevalent in bare soil areas than in regions adjacent to shrub patches [44]. A study on grasslands subjected to grazing has shown that overgrazing can lead to the replacement of grasses by shrub species [45]. Therefore, if herb plants remain undisturbed, shrubs are unlikely to invade, and the boundary between shrubs and herbs is established through competition.

Biological Factors Change Suitability of Biogeographic Regions

When only environmental factors were considered, the mean values of the biogeographic regions remained unchanged upon the addition of biological factors; however, the value intervals of these regions changed (Fig. 5). This discrepancy may be attributed to the differing ecological adaptation strategies of the two plant types. Shrubs typically possess deeper root systems and lignified tissues, which confer an advantage in withstanding harsh environments during resource acquisition and under environmental stress.

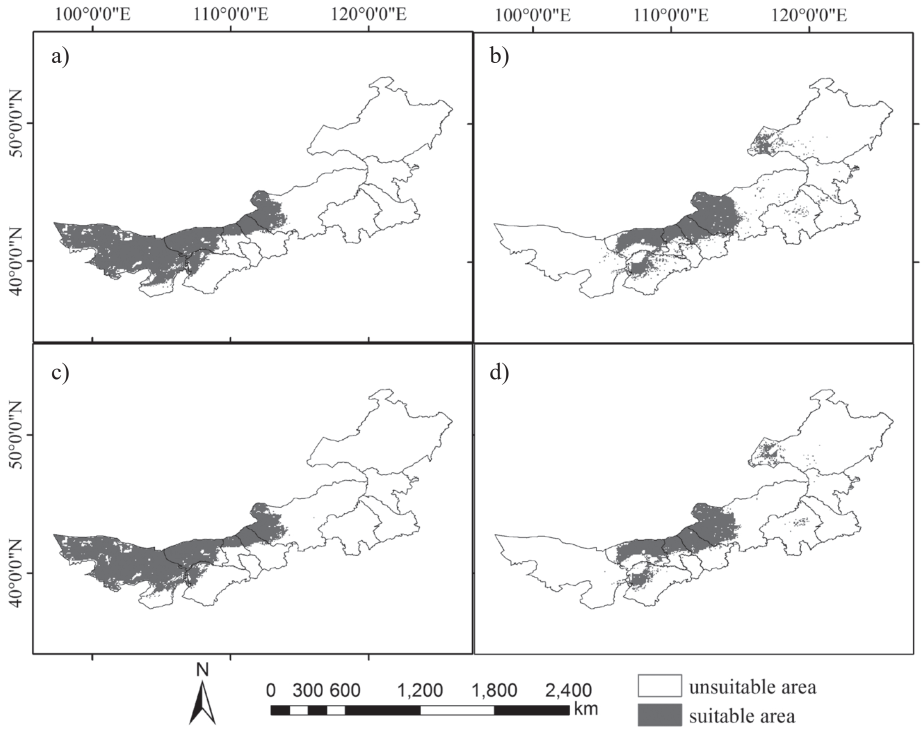

Fig. 4. Effects of different influencing factors on the distribution area of shrub and herb regions.
Note: a) is the distribution map of the shrub region affected by environmental factors; b) is the distribution map of the herb region affected by environmental factors; c) is the distribution map of the shrub region affected by environmental and biological factors; d) is the distribution map of the herb region affected by environmental and biological factors.

In contrast, although herb plants exhibit rapid growth and high reproductive capacity, they are more sensitive to environmental fluctuations [41].

Suitability refers to the ability of a species to survive, reproduce, and establish stable populations under specific environmental conditions. Habitat suitability is a crucial factor in the successful establishment of translocated populations [46]. The suitability predicted by the MaxEnt model illustrates the relationship between species and environmental factors, but does not account for interspecific relationships. The suitability of biogeographic regions may vary owing to the presence of interspecific competition.

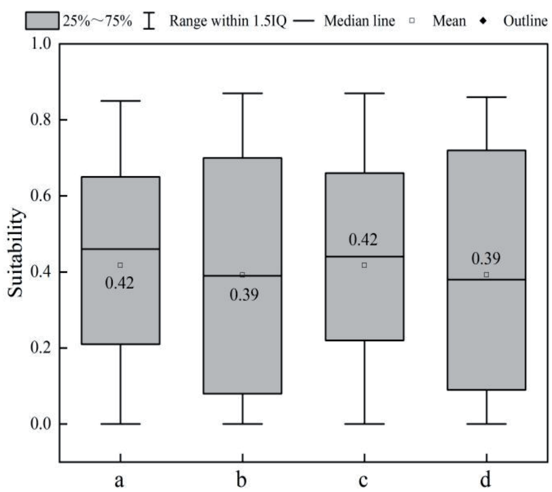

Fig. 5. Effects of different influencing factors on the distribution of suitability in shrub and herb regions.
Note: The annotations for a, b, c, and d are shown in Fig. 4.

The Implications and Limitations of This Work

Integrating the bidirectional interaction effects between shrubs and herbs into the MaxEnt model can enhance our understanding of the "shrub expansion-grassland degradation" process. Traditional species distribution models only consider species' responses to environmental gradients, thus shrub expansion has often been attributed solely to climate change, such as shifts in precipitation. The model developed in this study reveals that the suitability of the herb layer has become the second most dominant factor influencing shrub distribution. This indicates that shrub expansion is driven not only by climate but is also linked to the herb community. Shrubs affect the survival of herbs by altering local conditions, such as soil moisture and nutrients, while the herb community, in turn, influences shrub establishment.

The climate data used in this research process were derived from the average of 1990-2000. Due to the stability of the average climatic state, this research process is reasonable. During this study, it was found that the shrub area and the herb area had overlap only in ecological niches for precipitation factors, which might be due to the low accuracy of environmental data. Therefore, in future research, high-precision environmental data can be utilized for modeling. In our research, the relationship between the distribution regions of shrubs and herbs at the regional scale was mainly analyzed. In future studies, potential competition among plants will be considered, such as incorporating allelopathic factors into the analysis of interspecific relationships.

Conclusions

Based on the MaxEnt model, the biogeographic regions within the shrub and herb areas of the desert-steppe region were simulated, and the influence of biological factors on the distribution of these regions was analyzed. The following results were obtained: (i) the accuracy of the model, as indicated by the AUC values, for the shrub and herb regions exceeded 0.85, demonstrating a strong model performance; (ii) biological interactions were identified as significant limiting factors for the distribution of biogeographic regions; (iii) among the primary influencing factors, the shrub and herb regions competed solely for Bio13 resources; (iv) when biological factors were incorporated, the distribution areas of the shrub and herb regions decreased compared to scenarios where only environmental factors were considered; and (v) the mean value of regional suitability remained unaffected by biological factors.

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Author Contributions

Conceptualization: SF, CFZ. Methodology: SF, CFZ, BW. Formal analysis: HSZ, LM. Writing – original draft preparation: SF. Writing – review and editing: CFZ. Visualization: HSZ. Supervision: BW.

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Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on request.

Conflict of Interest

The authors declare no conflict of interest.

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