

Original Research

Distribution Shifts of *Rhodiola kirilowii* on the Tibetan Plateau under Anthropogenic and Future Climate Drivers

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Abstract

The sustainable development of Tibetan Plateau plant resources is threatened by global climate change. *Rhodiola* species, valuable in traditional Tibetan medicine, thrive in harsh high-altitude environments but face overharvesting pressure. This study applied the MaxEnt model to project the potential distribution of *Rhodiola kirilowii* and assess the impacts of future climate change and human activities on its range and habitat centroid. Results show that *R. kirilowii* is currently concentrated along the borders of Qinghai, Gansu, Sichuan, Yunnan, and Tibet. Human activities have substantially reduced suitable habitat area. Under future climate scenarios (2050s and 2070s; SSP126, SSP245, and SSP585), suitable habitats are projected to expand northwestward, with a notable overall area increase, especially in high-altitude zones. The distribution centroid also shifts northwest, reflecting close links between species distribution and environmental changes. These findings offer key insights into the ecological adaptation and future distribution of *Rhodiola* species, while supporting conservation and sustainable use planning for wild *R. kirilowii*.

Keywords: *Rhodiola kirilowii*, MaxEnt model, climate change, human activities, potential suitable habitat

Introduction

Climatic conditions play a key role in determining species distributions [1]. Global warming is driving plant species to migrate to higher altitudes [2], while trends toward warmer and wetter conditions are impacting plant growth [3, 4]. Currently, the global

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temperature is increasing at a rate of 0.2°C per decade [2], while both temperature and precipitation on the Tibetan Plateau show an upward trend [5], with the most pronounced warming occurring in high-altitude regions [6]. In recent years, human activities have driven global warming, triggering a series of climatic changes including global biodiversity loss, ecological community reorganization, and sea-level rise, which have damaged the habitats of many species [7, 8]. Habitats play a crucial role in the survival and reproduction of species [9], and their alteration is a major cause of biodiversity loss [10]. Changes in habitat are influenced by many factors, with the two primary drivers being climate change and human activities [11]. The distribution of alpine plants is particularly susceptible to human activities. As an important pastoral region, the intensity of grazing on the Tibetan Plateau exerts varying impacts on alpine plant distribution. Moderate, long-term, and winter grazing have been shown to help maintain or even enhance alpine species richness and diversity [12, 13], whereas overgrazing leads to grassland degradation [14]. Beyond this, overexploitation is a major driver of global biodiversity decline [15]. Unsustainable harvesting and habitat destruction pose serious threats to medicinal plants [16]. However, the current China Red List underestimates the threat of overharvesting linked to trade [17]. These anthropogenic disturbances, interacting with climate change, directly or indirectly alter the ecological environment of the Tibetan Plateau, leading to shifts in the distribution patterns of specific taxa such as *Rhodiola* species [18]. Therefore, a scientific assessment of the factors affecting species distribution must take into account the influence of human activities.

Rhodiola, a key genus within the Crassulaceae family, comprises 73 species widely distributed across China, except in the central, eastern, and southern regions [19]. Representative species such as *Rhodiola kirilowii* (Regel) Maxim., *Rhodiola crenulate* (HK. f. et Thoms.) H. Ohba, *Rhodiola tangutica* (Maxim.) S. H. Fu, and *Rhodiola fastigiata* (Hook. f. & Thomson) S. H. Fu are important sources of traditional Tibetan medicine, known for their effects in clearing heat, detoxifying, calming the mind, relieving cough, reducing blood stasis, stopping bleeding, alleviating altitude sickness, and enhancing cold resistance [20]. Since 1976, extensive research has been conducted on this genus [21], leading to the identification of over 60 active components classified into nine categories [22]. Salidroside and its aglycone, tyrosol, serve as key quality markers due to their medicinal values, including antioxidant, anti-fatigue, anti-hypoxia, antiviral, and cardioprotective properties [22-27]. Current studies primarily focus on the medicinal value and cultivation techniques of *Rhodiola* species [20, 21, 28], while the response mechanisms of their suitable habitats to climate change and human activities remain poorly understood. Particularly in the highly climate-sensitive Tibetan Plateau region, the distribution shifts and sustainable

utilization potential of *R. kirilowii* have not yet been systematically analyzed.

Niche models utilize species occurrence data and environmental variables to simulate potential species distributions based on mathematical algorithms [29]. Currently, models applied in species distribution research include Ecological Niche Factor Analysis (ENFA), BIOCLIM, DOMAIN, Genetic Algorithm for Rule-set Production (GARP), and Maximum Entropy (MaxEnt) [30]. Among these, the MaxEnt model demonstrates high accuracy and stability even with limited species occurrence records, shows strong agreement with actual distributions, and is user-friendly and sensitive. It is widely used in predicting and conserving endangered species, monitoring invasive species, and projecting species distributions under future climate scenarios [31-33]. Due to its high predictive accuracy, minimal parameter requirements, and operational simplicity, MaxEnt has garnered significant attention and application.

This study investigated *Rhodiola kirilowii* using the MaxEnt model to predict its current and future suitable habitats. Given the significant impact of human activities on species distribution, the human footprint index was incorporated into the modeling. Two models were constructed: one incorporating human activities and one excluding them, to assess their effects on the distribution of suitable habitats for *R. kirilowii*. A comparative analysis was conducted to evaluate whether human activities dominate its distribution, providing a theoretical basis for the conservation, development, and sustainable utilization of *R. kirilowii* on the Tibetan Plateau.

Materials and Methods

Acquisition and Processing of *Rhodiola kirilowii* Distribution Data

Distribution data of *Rhodiola kirilowii* were obtained from four sources: (1) field surveys conducted in July 2023; (2) the Chinese Virtual Herbarium (CVH, <https://www.cvh.ac.cn/>) accessed in December 2023; (3) the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>) and (4) the National Specimen Information Infrastructure (NSII, <http://www.nsii.org.cn/2017/homeMobile.php>), also accessed in December 2023. A total of 652 distribution points of *R. kirilowii* on the Tibetan Plateau were collected. The data were processed using Excel 2016 and saved in CSV format. Redundant records were removed with ENMTools, retaining only one occurrence per 5 km×5 km grid. Finally, 123 valid distribution points were retained (Fig. 1) [34].

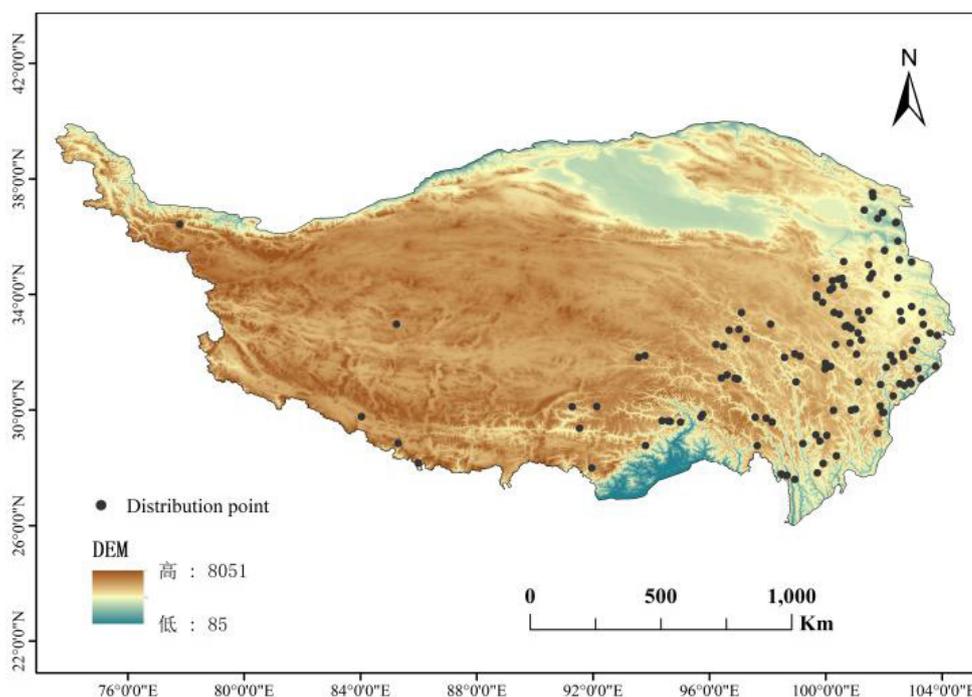


Fig. 1. Distribution points of *Rhodiola kirilowii* on the Tibetan Plateau.

Acquisition and Processing of Environmental Data

This study incorporated 32 environmental variables (Table 1), including 19 bioclimatic factors, 9 soil factors, 3 topographic factors, and 1 human activity factor, all at a resolution of 2.5 arc-minutes. Current and future climate data were obtained from the WorldClim database (<http://worldclim.org/data/index.html>). Three Shared Socioeconomic Pathways (SSPs) were adopted: SSP126 (low-emission sustainable scenario), SSP245 (medium-emission scenario), and SSP585 (high-emission fossil fuel-dependent scenario) [35]. Topographic data were sourced from the Geospatial Data Cloud (<https://www.gscloud.cn/>). Soil factor data were derived from the Harmonized World Soil Database (HWSD) of the Food and Agriculture Organization (<http://www.fao.org/faostat/en/#data>). Human activity data were obtained from the 2022 human footprint index provided by Mu et al. (<https://doi.org/10.6084/m9.Figs.hare.16571064>), which includes eight variables: population density, nighttime light, built environment, cropland, pastureland, roads, railways, and navigable waterways [36].

To avoid overfitting and bias caused by multicollinearity among the 32 ecological factors, the MaxEnt model was run 10 times for each variable, and factors with zero contribution were excluded [37]. The Pearson correlation coefficient (r) was calculated using ENMTools. Factors with $|r| < 0.8$ were preliminarily selected. For variables with $|r| \geq 0.8$, ecologically redundant factors with lower contributions were removed based on the biological characteristics of *Rhodiola kirilowii* [38]. Topographic factors were retained due to

their significant influence on species distribution in the unique terrain of the Tibetan Plateau [39]. Ultimately, 15 ecological factors were selected for the model, excluding human activities (Table 2), and 9 factors were chosen for the model, including human activities (Table 3).

Model Construction and Parameter Optimization

This study employed MaxEnt 3.4.4 to predict changes in current and future suitable habitats for *Rhodiola kirilowii*. Due to interspecific variations in environmental adaptability and physiological traits, models constructed with default parameters in MaxEnt often yield predictions with limited accuracy and reliability [40]. The key factors influencing model predictive performance are the regularization multiplier (RM) and feature combination (FC) [41]. Model optimization was performed using the "Kuenm" package in R [42], with RM tested at eight levels (0.5-4.0 in increments of 0.5) and FC set to L, H, LQ, and LQH, resulting in 32 distinct parameter combinations. Model selection was based on the ROC curve, OR10, and AICc. Statistically significant models were retained initially, followed by filtering for those with an omission rate $< 5\%$. Among these, models with a delta AICc value of 0 were selected. The model with the smallest delta AICc value achieved an optimal balance between complexity and predictive capability.

Table 1. List of environmental factors.

Environmental Factor Type	Code	Description
Bioclimatic Factors	Bio-1	Annual Mean Temperature (°C)
	Bio-2	Mean Diurnal Range (°C)
	Bio-3	Isothermality (%)
	Bio-4	Temperature Seasonality
	Bio-5	Max Temperature of Warmest Month (°C)
	Bio-6	Min Temperature of Coldest Month (°C)
	Bio-7	Temperature Annual Range (°C)
	Bio-8	Mean Temperature of Wettest Quarter (°C)
	Bio-9	Mean Temperature of Driest Quarter (°C)
	Bio-10	Mean Temperature of Warmest Quarter (°C)
	Bio-11	Mean Temperature of Coldest Quarter (°C)
	Bio-12	Annual Precipitation (mm)
	Bio-13	Precipitation of Wettest Month (mm)
	Bio-14	Precipitation of Driest Month (mm)
	Bio-15	Precipitation Seasonality
	Bio-16	Precipitation of Wettest Quarter (mm)
	Bio-17	Precipitation of Driest Quarter (mm)
	Bio-18	Precipitation of Warmest Quarter (mm)
	Bio-19	Precipitation of Coldest Quarter (mm)
Soil Factors	T_CACO3	Topsoil Calcium Carbonate
	T_CASO4	Topsoil Gypsum
	T_CLAY	Subsoil Clay Fraction
	T_GRAVEL	Subsoil Gravel Content
	T_OC	Topsoil Organic Carbon
	T_PH_H2O	Topsoil pH (H ₂ O)
	T_REF_BULK	Topsoil Reference Density Bulk
	T_SAND	Subsoil Sand Fraction
	T_SILT	Subsoil Silt Fraction
Topographic Factors	Elev	Altitude (m)
	Slope	Slope (°)
	Aspect	Aspect
Human Footprint	HFP	The Global Human Footprint

Model Accuracy Evaluation

In the MaxEnt model, species occurrence data and environmental variables of *Rhodiola kirilowii* were incorporated, with the occurrence records randomly partitioned into 75% for training and 25% for testing, using 10 replicate runs. The area under the receiver operating characteristic curve (AUC) was employed to evaluate model performance [43]. The AUC value ranges

from 0 to 1, with values above 0.7 considered acceptable and higher values indicating better predictive accuracy.

Delimitation of *Rhodiola kirilowii* Suitable Habitat and Centroid Migration

Based on the MaxEnt model results and referring to the method by Cantor et al. [44], a specificity threshold of 0.1785 was determined. Four suitability levels

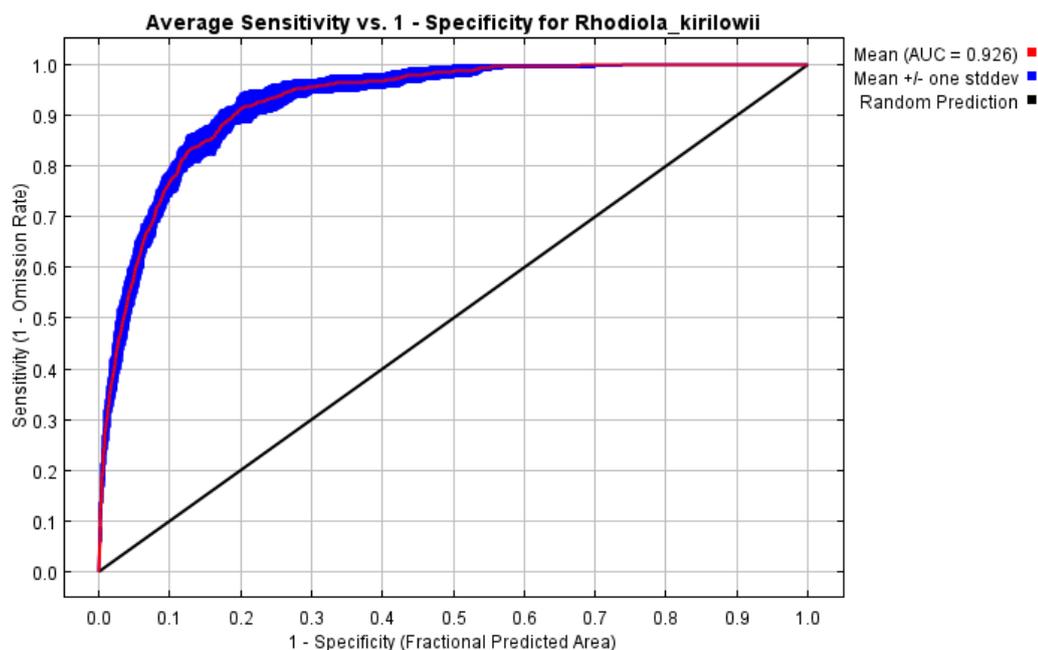


Fig. 2. ROC curve verification of MaxEnt model prediction results without human footprint.

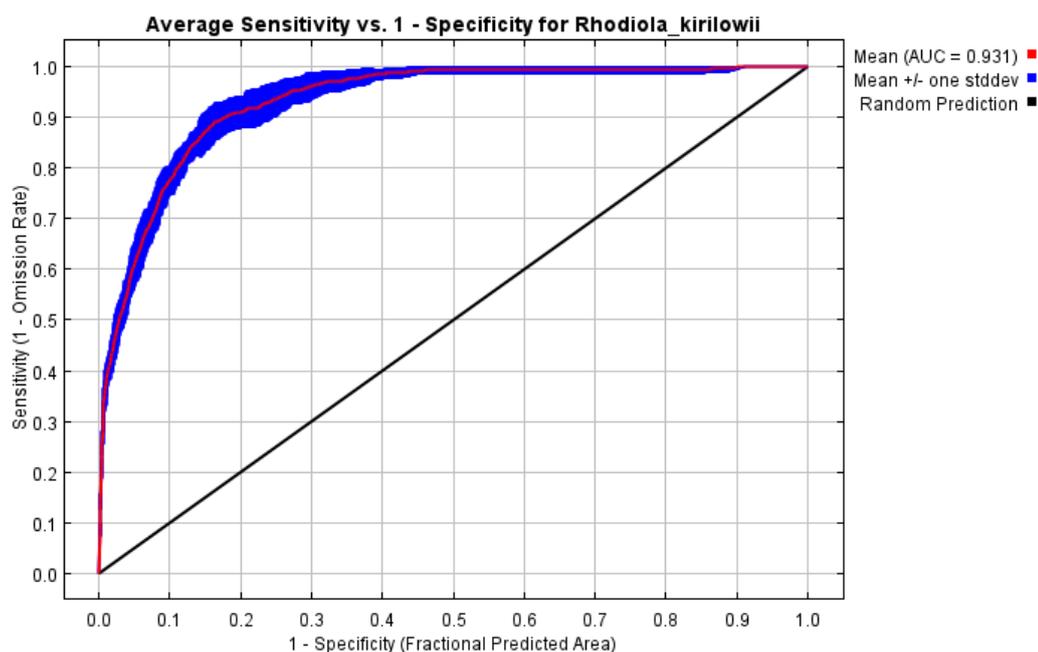


Fig. 3. ROC curve verification of MaxEnt model prediction results with human footprint.

were classified using ArcGIS: unsuitable habitat [0, 0.1785], low-suitability habitat [0.1785, 0.4], medium-suitability habitat [0.4, 0.6], and high-suitability habitat [0.6, 1]. The same classification was applied to future distribution predictions. The area of each suitability class was calculated using the Zonal Statistics tool in the Spatial Analysis toolbox of ArcGIS. By comparing current and future distributions, changes in the area of each suitability class across different periods were quantified. The core distribution areas of *Rhodiola*

kirilowii were identified by reducing suitable habitats under each climatic scenario to a single centroid point. Centroid shifts were analyzed using the Point Merge and Point to Line tools in ArcGIS.

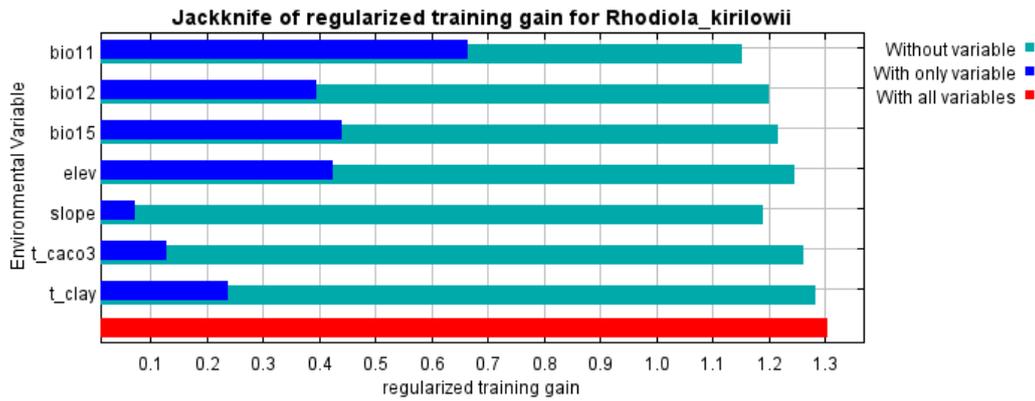


Fig. 4. Jackknife of regularized training gain for *Rhodiola_kirilowii* without human activities.

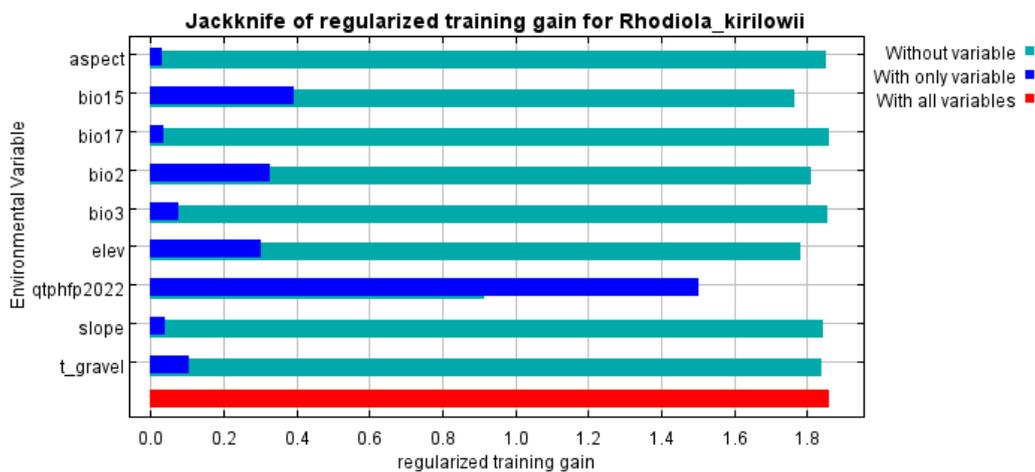


Fig. 5. Jackknife of regularized training gain for *Rhodiola_kirilowii* under human activities.

Results and Discussion

MaxEnt Model Prediction and Accuracy Verification

Model optimization results showed that, in the absence of human activities, the optimal feature combination was LQPT with a regularization multiplier of 1.8; under the influence of human activities, the optimal feature combination was LQ with a regularization multiplier of 0.6. Under these optimized parameter settings, the mean AUC value for the current climate without human activity factors was 0.926 (Fig. 2). For the 2050s and 2070s under SSP126, SSP245, and SSP585 scenarios, the mean AUC values were 0.913, 0.911, 0.902 (2050s) and 0.904, 0.906, 0.907 (2070s), respectively. With human activity factors included, the mean AUC value for the current climate was 0.931 (Fig. 3), while for the 2050s and 2070s under the same scenarios, the values were 0.930, 0.932, 0.932 (2050s) and 0.931, 0.933, 0.933 (2070s), respectively. All AUC values exceeded 0.9, indicating excellent predictive accuracy and high reliability of the model.

Main Environmental Factors Influencing *Rhodiola_kirilowii* Distribution

The top four environmental factors with the highest contribution rates were selected as the dominant environmental factor combination. Results based on percent contribution, permutation importance, and jackknife tests showed that, in the absence of human activities (Fig. 4), the top four factors each had a contribution rate exceeding 15%. These were: mean temperature of the coldest quarter (bio11), annual precipitation (bio12), elevation (elev), and precipitation seasonality (bio15), with a cumulative contribution rate of 89.1%. Thus, the dominant environmental factors influencing the potential suitable habitat distribution of *Rhodiola_kirilowii* under no human activity were identified as mean temperature of the coldest quarter, annual precipitation, elevation, and precipitation seasonality.

Under the influence of human activities (Fig. 5), the top four contributing factors were, in descending order: human footprint data (hfp2022), mean diurnal temperature range (bio2), precipitation seasonality (bio15), and elevation (elev), with a cumulative

Table 2. Percentage contribution and permutation importance values of environmental factors for *Rhodiola kirilowii* without human activities.

Environmental factors	Contribution rate (%)	Permutation importance (%)
bio_11	31.2	36.8
bio_12	24.3	16.6
elev	19.3	13.5
bio_15	14.3	13.5
slope	7.0	12.3
t_clay	2.3	2.4
t_caco3	1.5	4.8

Table 3. Percentage contribution and permutation importance values of environmental factors for *Rhodiola kirilowii* under human activities.

Environmental factors	Contribution rate (%)	Permutation importance (%)
hfp_2022	73.0	72.6
bio_2	13.5	7.3
bio_15	6.0	14.7
elev	2.6	2.4
t_gravel	1.4	1.0
bio_17	1.4	0.1
slope	1.2	0.8
aspect	0.4	0.5
bio_3	0.4	0.6

contribution rate of 95.1%. Thus, the dominant environmental factors influencing the potential suitable habitat distribution of *Rhodiola kirilowii* under human activities were identified as human activities, mean diurnal temperature range, precipitation seasonality, and elevation.

A comparison of the two simulation scenarios revealed that precipitation seasonality (bio15) and elevation (elev) maintained high contribution rates in both cases. After incorporating human activities, the human footprint factor (hfp2022) exhibited the highest contribution rate at 73%. In contrast, the contribution rates of mean temperature of the coldest quarter (bio11) and annual precipitation (bio12) decreased significantly, while the contribution rate of mean diurnal temperature range (bio2) increased.

Response Curves of Key Factors Influencing *Rhodiola kirilowii* and Species Presence Probability

Response curves of the dominant environmental factors affecting the distribution of *Rhodiola kirilowii* under the scenario without human activities in the MaxEnt model are shown in Fig. 6. The curves reflect the relationship between these factors and the probability of *R. kirilowii* occurrence. The results indicate that, in the absence of human activities, the relationship between the probability of distribution and both the mean temperature of the coldest quarter (bio11) and annual precipitation (bio12) follows a unimodal curve. As these environmental factors increase, the probability of distribution initially rises, reflecting increased sensitivity or adaptability, peaks at an optimal value, and then declines. In contrast, the relationship between distribution probability and both elevation (elev) and precipitation seasonality (bio15) exhibits a declining curve. As these factors increase, the distribution probability decreases, indicating reduced sensitivity or adaptability.

Using a suitability threshold >0.5 to define the suitable growth range, the mean temperature of the coldest quarter (bio11), which had the greatest impact on the distribution of *Rhodiola kirilowii*, showed an optimal range of -10 to 0°C, with the most suitable value at 0°C. Annual precipitation (bio12) also significantly influenced the distribution, with a suitable range of 200-400 mm and an optimal value of 300 mm. Precipitation seasonality (bio15) followed, with a suitable range of 35-42 mm and an optimal value of 35 mm. Elevation (elev) also played an important role, with a suitable range of 3300-3800 m and an optimal value of 3600 m.

Response curves of the dominant environmental factors affecting the distribution of *Rhodiola kirilowii* under human activities are shown in Fig. 7. The results indicate that the relationship between the probability of distribution and both precipitation seasonality (bio15) and elevation (elev) follows a unimodal curve. As these factors increase, the distribution probability initially rises, reflecting increased sensitivity or adaptability, peaks at an optimal value, and then declines. In contrast, the relationship with mean diurnal temperature range (bio2) exhibits a declining curve, where the distribution probability decreases with increasing values, indicating reduced sensitivity or adaptability. The relationship with human activities (hfp2022) shows an increasing curve: the distribution probability rises with greater human influence, reflecting enhanced sensitivity or adaptability, and plateaus after reaching its optimum.

Among these factors, human activities (hfp2022) had the greatest impact on the distribution of *Rhodiola kirilowii*, exhibiting a peak at a value of 25. Mean diurnal temperature range (bio2) also significantly influenced the distribution, with an optimal value of 52°C. Precipitation seasonality (bio15) followed, with a suitable range of 50-70 mm and an optimal value of 60 mm. Elevation (elev) also played an important role, with

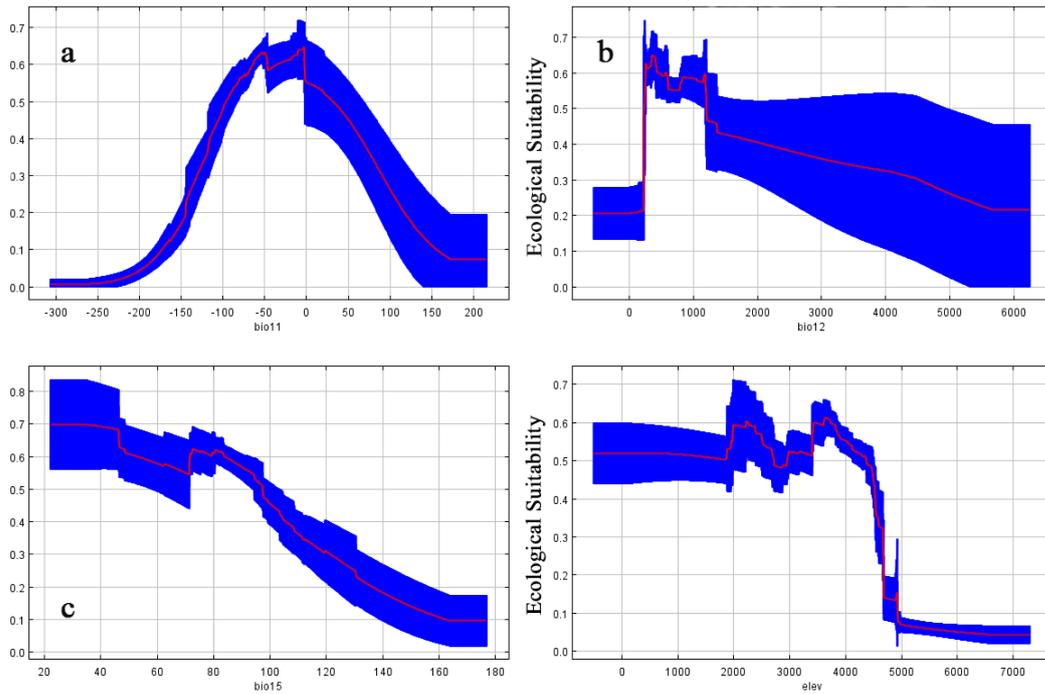


Fig. 6. Response curve of dominant environmental factors of *Rhodiola kirilowii* without human activities. a) Mean temperature of coldest quarter, b) annual precipitation, c) precipitation seasonality, d) altitude.

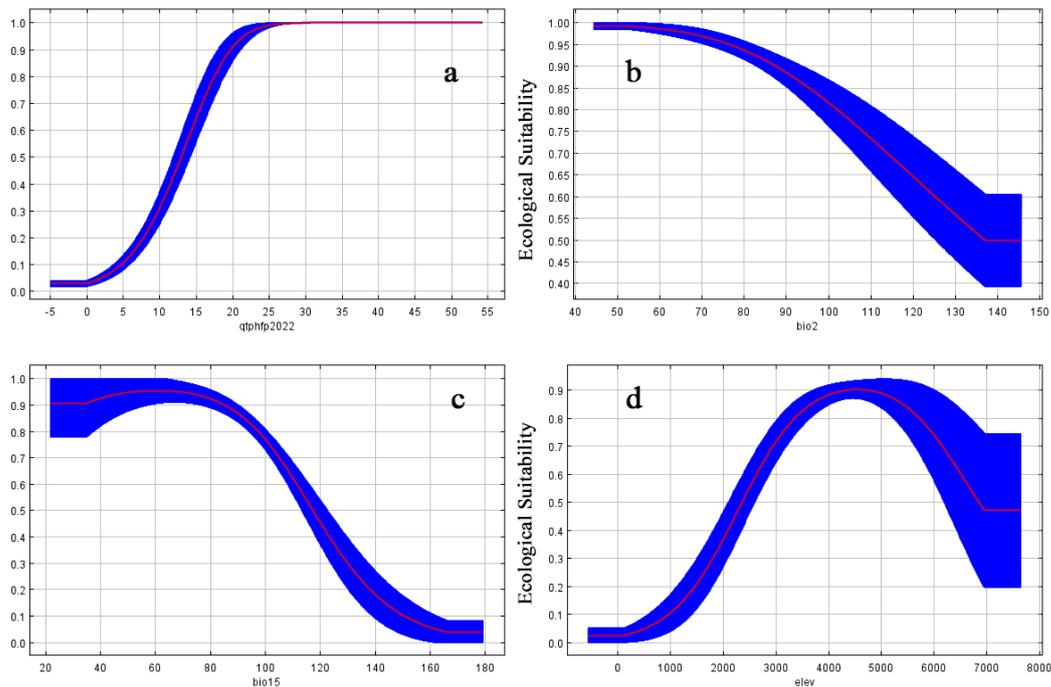


Fig. 7. Response curve of dominant environmental factors of *Rhodiola kirilowii* under human activities. a) The global human footprint, b) mean diurnal range, c) precipitation seasonality, d) altitude.

a suitable range of 4000-5000 m and an optimal value of 4500 m.

A comparison of the two simulation scenarios revealed the most notable difference in suitable elevation ranges. Under the scenario without human activities, the model indicated that *Rhodiola kirilowii* predominantly

thrives at lower elevations. When human activities were incorporated, the results demonstrated a significant influence on the suitable elevation selection for the species. Specifically, the inclusion of human activities led to a marked increase in the suitable elevation range

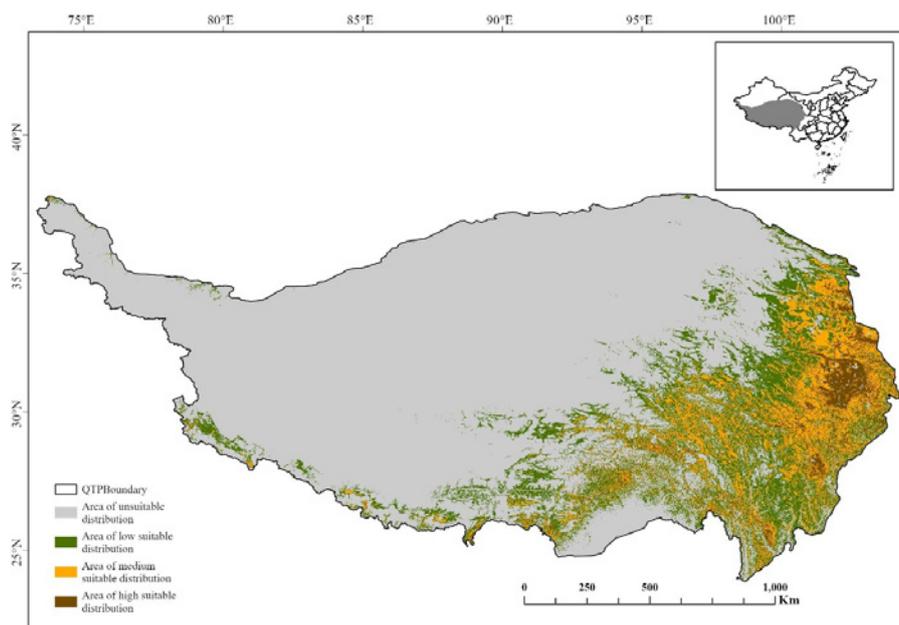


Fig. 8. Suitable habitat areas of *Rhodiola kirilowii* in the Tibetan Plateau under the current climate without human activities.

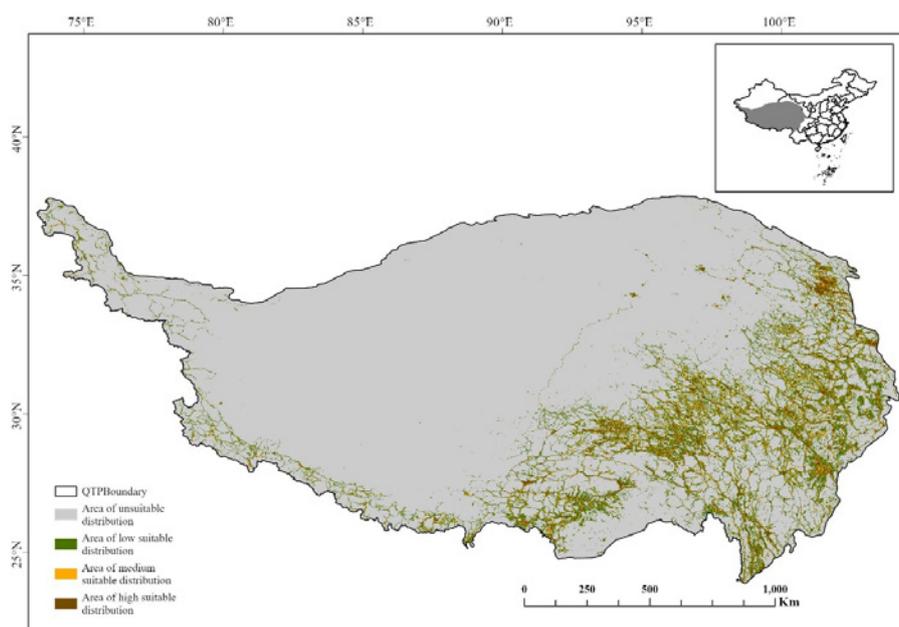


Fig. 9. Suitable habitat areas of *Rhodiola kirilowii* in the Tibetan Plateau under the current climate with human activities.

for *R. kirilowii*, with the optimal elevation rising by 900 m.

Suitable Habitat of *Rhodiola kirilowii* in the Qinghai-Tibetan Plateau under Current Climate Scenarios

Under current climate conditions without human activities, *Rhodiola kirilowii* is primarily distributed in the border regions of Qinghai, Gansu, Sichuan, Yunnan, and Tibet (Fig. 8). The total suitable habitat

area is 6.407×10^5 km², accounting for approximately 38.7% of the Tibetan Plateau. Specifically, the areas of high, medium, and low-suitability habitats are 0.737×10^5 km² (11.5%), 2.156×10^5 km² (33.7%), and 3.514×10^5 km² (54.8%), respectively (Table 4). High-suitability areas are concentrated in Haidong City of Qinghai, Gannan Prefecture of Gansu, Aba and Garze Prefectures of Sichuan, and Diqing Tibetan Autonomous Prefecture of Yunnan, with the highest density at the border between Gansu and Sichuan (Gannan and Aba Prefectures). Medium-suitability areas are mostly

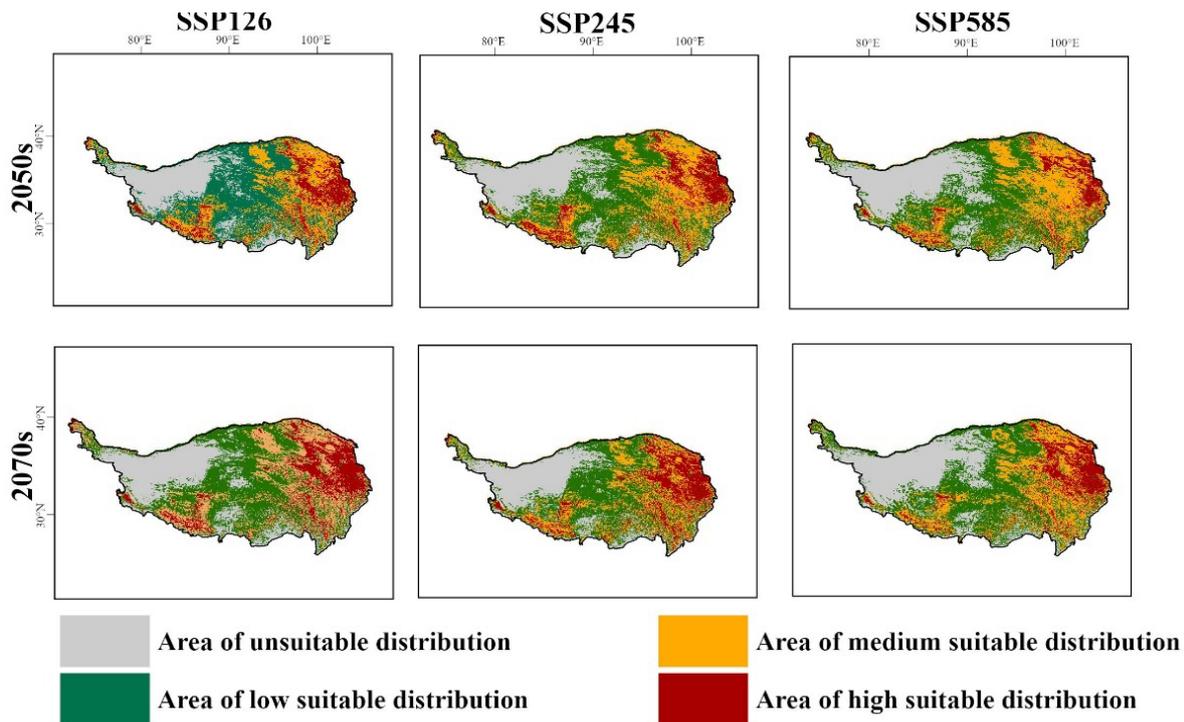


Fig. 10. Suitable habitat areas of *Rhodiola kirilowii* in the Tibetan Plateau under different climatic scenarios in the 2050s and 2070s without human activities.

distributed in northwestern Sichuan and the junction of Qinghai, Gansu, and Sichuan, with additional patches in southeastern Tibet and northwestern Yunnan. Low-suitability areas are predominantly found in southeastern Qinghai and southwestern Sichuan, with minor distributions in central, southeastern, and southwestern Tibet, southwestern Xinjiang Uygur Autonomous Region, and northwestern and southwestern Gansu.

Under current climate conditions with human activities, *Rhodiola kirilowii* remains primarily distributed in the border regions of Qinghai, Gansu, Sichuan, Yunnan, and Tibet (Fig. 9). The total suitable habitat area is 3.353×10^5 km², accounting for approximately 38.7% of the Tibetan Plateau. Specifically, the areas of high, medium, and low-suitability habitats are 0.514×10^5 km² (15.3%), 0.651×10^5 km² (19.4%), and 2.188×10^5 km² (65.3%), respectively (Table 5). High-suitability areas are scattered across northwestern Sichuan, southeastern and southwestern Tibet, eastern and southeastern Qinghai, and northwestern Yunnan. Medium-suitability areas show a similar distribution pattern to the high-suitability zones. Low-suitability areas are predominantly concentrated in southern Qinghai, southeastern Tibet, northwestern Sichuan, and northwestern Yunnan, with minor distributions in southwestern Xinjiang Uygur Autonomous Region and from southern to southwestern Tibet.

A comparison of the two simulation scenarios reveals that the distribution patterns of suitable habitats for *Rhodiola kirilowii* are broadly similar. However, under the influence of human activities, the total area of suitable habitats is significantly reduced. The quality of

these habitats also declines, characterized by a decrease in medium-suitability areas and an increase in low-suitability areas. The spatial concentration of high-suitability zones shifts, becoming more clustered around Xining City.

Potential Distribution Areas of *Rhodiola kirilowii* in the Qinghai-Tibetan Plateau under Three Future Climate Scenarios

The MaxEnt model was used to predict the potential geographical distribution of *Rhodiola kirilowii* in the Qinghai-Tibetan Plateau under three climate scenarios (SSP126, SSP245, SSP585) for the 2050s and 2070s (Fig. 10 and Fig. 11).

In the absence of the influence of human activities, the potential distribution area of *Rhodiola kirilowii* significantly increased, showing a substantial growth trend. Specifically,

In the 2050s:

Under the SSP126 scenario, the high suitability area expanded significantly towards the central Qinghai-Tibetan Plateau, with an expansion rate of 344.37%. The main expansion areas were northwestern Sichuan Province, eastern Qinghai Province, Gansu Province, Tibet, and southwestern Xinjiang Uygur Autonomous Region. The medium suitability area expanded widely in eastern, southwestern, and small parts of northwestern Qinghai-Tibetan Plateau, with an expansion rate of 206.3%. The low suitability area expanded mainly in the border regions of Tibet, Qinghai Province, and Xinjiang Uygur Autonomous Region, with an expansion rate of

Table 4. Area of potential suitability for *Rhodiola kirilowii* under different future climate without human activities ($\times 10^4$ km²).

Climate Scenario	Period	Low Suitability Area	Area Change (%)	Medium Suitability Area	Area Change (%)	High Suitability Area	Area Change (%)	Total Area	Area Change (%)
Current	1979-2013	35.1	-	21.6	-	7.4	-	64.1	-
SSP126	2050s	95.1	170.6	66.0	206.3	32.8	344.4	193.9	26.1
	2070s	91.9	161.6	61.7	186.0	39.0	428.6	192.5	42.1
SSP245	2050s	90.9	158.7	67.7	214.1	29.1	295.1	187.7	32.9
	2070s	88.1	150.7	57.3	165.9	42.1	471.8	187.6	49.6
SSP585	2050s	90.3	156.9	72.4	235.5	20.6	180.1	183.3	35.9
	2070s	89.8	155.5	59.8	177.2	30.8	317.8	180.3	41.3

170.60%. The total area increased by 26.55% compared to the current period.

Under the SSP245 scenario, most of the high suitability area expanded towards central Qinghai Province and its border with Gansu Province, with significant expansion also in the southwestern and northwestern Qinghai-Tibetan Plateau, covering an area of 3.159×10^5 km², with an expansion rate of 428.63%. The expansion trends for medium and low suitability areas were similar to the SSP126 scenario, with area increase rates of 214.05% and 158.68%, respectively. The total area increased by 32.85% compared to the current period.

Under the SSP585 scenario, the medium suitability area showed the largest expansion, primarily in Qinghai Province, northwestern Sichuan Province, and central to southern Tibet, with an expanded area of 5.087×10^5 km² and an expansion rate of 235.52%. The expansion trends for high and low suitability areas were similar to the SSP245 scenario, but with smaller expanded areas, at expansion rates of 180.05% and 156.86%, respectively. The total area increased by 35.93% compared to the current period.

In the future 2070s:

Compared to the 2050s, the overall trend for the distribution areas of *Rhodiola kirilowii* under SSP126, SSP245, and SSP585 climate scenarios was a significant increase in high suitability areas, with a slight decrease in medium and low suitability areas. The expansion of high suitability areas was most pronounced at the border of Qinghai, Sichuan, and Gansu provinces, showing a trend of diffusion towards the northwest of the Qinghai-Tibetan Plateau. The most significant increases and decreases in low suitability areas were observed in Nagqu City of Tibet and Yushu Prefecture, Golmud City, and Haixi Prefecture of Qinghai.

Under the SSP126 scenario, the suitable area significantly decreased. The total area increased by 42.11% compared to the current period.

Under the SSP245 scenario, low suitability areas significantly decreased in Haixi Prefecture but significantly expanded in Nagqu City and Golmud City.

The total area increased by 49.62% compared to the current period.

Under the SSP585 scenario, the total area of low suitability areas slightly decreased, with a reduction in distribution in Yushu Prefecture and a significant increase in Haixi Prefecture and Nagqu City. The total area increased by 41.28% compared to the current period.

In the presence of the influence of human activities (Fig. 11, Table 5), the potential distribution areas of *Rhodiola kirilowii* also showed an expansion trend in the 2050s and 2070s, but similar to the current suitable area distribution, they appeared fragmented. Significant expansion was observed in Xigaze City of Tibet and Kizilsu Kirghiz Autonomous Prefecture of Xinjiang. The expansion of high suitability areas was more concentrated at the border between Haidong City and Xining City in Qinghai Province. Specifically,

In the 2050s:

Under the SSP245 scenario, medium and low suitability areas showed the largest expansion, with expansion rates of 152.69% and 178.52%, respectively. The total area increased by 165.79% compared to the current period.

Under the SSP585 scenario, the high suitability area showed the largest expansion, with an expansion rate of 74.90%. The total area increased by 142.11% compared to the current period.

Under the SSP126 scenario, medium and low suitability areas at the border of Xigaze City and Ngari Prefecture in Tibet showed more significant expansion. The total area increased by 141.81% compared to the current period.

In the future 2070s:

Under the SSP126 and SSP245 climate scenarios, the distribution areas of *Rhodiola kirilowii* expanded more significantly outwards compared to the 2050s. The expansion of low suitability areas remained higher than that of medium and high suitability areas, similar to the 2050s, and the total area increased.

Under the SSP126 scenario, the areas of all three suitability levels showed a clear outward expansion trend in southeastern Qinghai Province, southwestern Sichuan

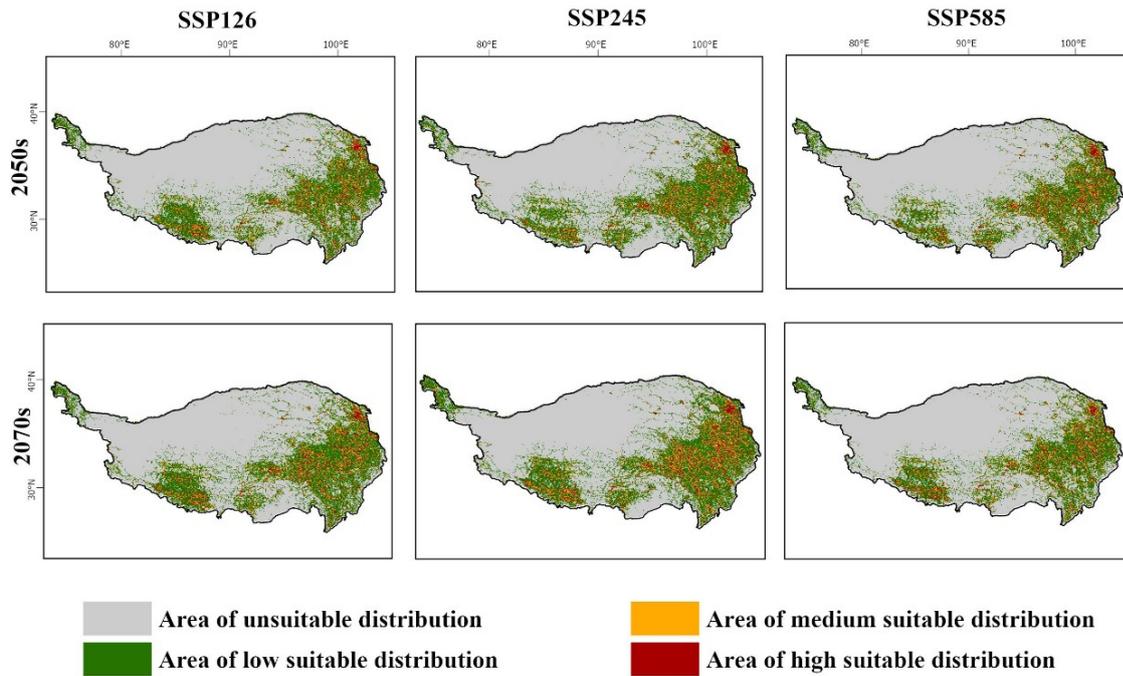


Fig. 11. Suitable habitat areas of *Rhodiola kirilowii* in the Tibetan Plateau under different climatic scenarios in the 2050s and 2070s with human activities.

Province, and eastern Tibet. The total area increased by 171.55% compared to the current period.

Under the SSP245 scenario, the suitable areas at the borders of Qinghai, Sichuan, Tibet, Gansu, and Yunnan provinces became denser. Medium and low suitability areas in Xigaze City and Ngari Prefecture in Tibet, and southwestern Xinjiang, showed significant expansion. The total area increased by 185.89% compared to the current period.

Under the SSP585 climate scenario, the areas of all three suitability levels were smaller than in the 2050s, and the total area slightly decreased. Suitable areas at the borders of Sichuan, Yunnan, and Tibet significantly decreased, while medium and low suitability areas in Xigaze City and Ngari Prefecture in Tibet, and southwestern Xinjiang, showed significant expansion, with a trend of suitable areas moving towards the

western Qinghai-Tibetan Plateau. The total area increased by 133.64% compared to the current period.

Despite climate change generally appearing to create more suitable habitats for *Rhodiola kirilowii* (total area expansion), the presence of human activities significantly altered the spatial pattern of this expansion, leading to fragmented distribution. This indicates that even when climate change presents new ecological opportunities, human land use and resource extraction remain major obstacles, preventing the species from fully capitalizing on these changes and potentially increasing its vulnerability due to habitat isolation.

Table 5. Area of potential suitability for *Rhodiola kirilowii* under different future climates with human activities ($\times 10^4$ km²).

Climate Scenario	Period	Low Suitability Area	Area Change (%)	Medium Suitability Area	Area Change (%)	High Suitability Area	Area Change (%)	Total Area	Area Change (%)
Current	1979-2013	21.9	-	6.5	-	5.1	-	33.5	-
SSP126	2050s	57.7	163.5	15.8	142.2	7.7	48.8	81.1	141.8
	2070s	64.3	193.8	17.5	168.1	9.3	81.1	91.1	171.6
SSP245	2050s	60.9	178.5	16.5	152.7	7.7	50.4	89.1	165.8
	2070s	64.2	193.3	20.2	210.5	11.5	123.4	95.9	185.9
SSP585	2050s	55.9	155.3	16.3	150.8	9.0	74.9	81.2	142.1
	2070s	53.9	146.3	15.8	143.2	8.6	67.5	78.3	133.6

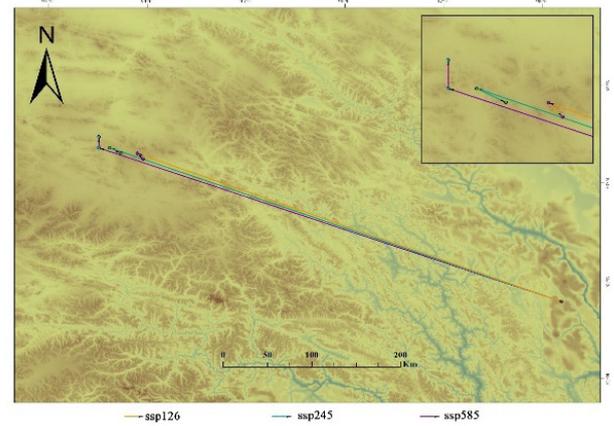
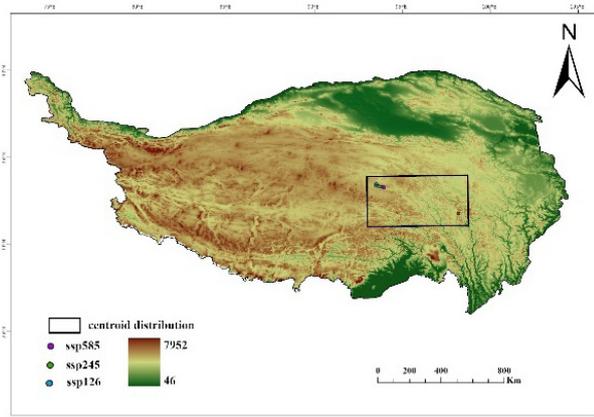


Fig. 12. Migration paths of *Rhodiola kirilowii* under different climates without human activities.

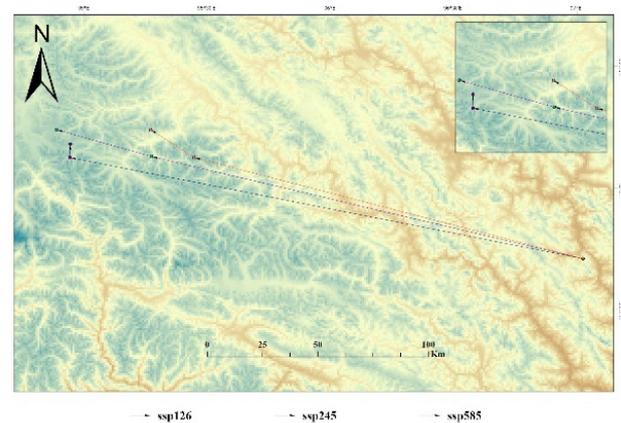
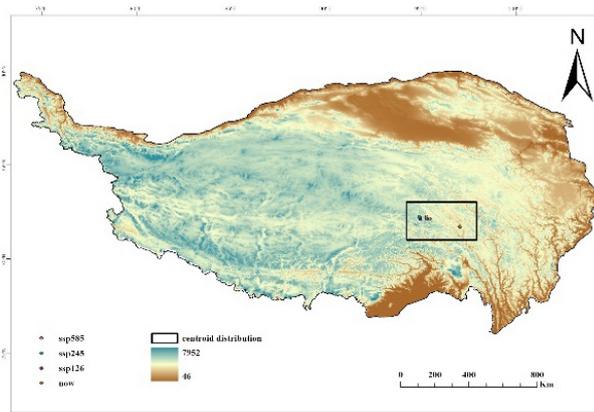


Fig. 13. Migration paths of *Rhodiola kirilowii* under different climates with human activities.

Centroid Migration of Potential Suitable Areas for *Rhodiola kirilowii* under Three Future Climate Scenarios

Centroid migration analysis revealed the spatial dynamics of the core suitable habitat areas for *Rhodiola kirilowii* under future climate scenarios.

In the absence of the influence of human activities (Fig. 12), the current centroid coordinates of *Rhodiola kirilowii* were 98.18887°E, 31.78831°N. In the 2050s, under all SSP climate scenarios, the centroid of *Rhodiola kirilowii* showed a trend of migrating northwestward. For example, under the SSP126 scenario, the centroid migrated 472.77 km northwestward, reaching coordinates 93.50564°E, 33.35683°N. However, in the 2070s, the migration direction diverged: under the SSP126 scenario, the centroid continued to migrate 12.41 km northward, reaching 93.50654°E, 33.46876°N; while under SSP245 and SSP585 scenarios, the centroid showed a trend of migrating southeastward (e.g., SSP245 migrated 12.25 km southeastward to 93.73241°E, 33.30158°N; SSP585 migrated 8.11 km southeastward to 93.95427°E, 33.24489°N).

In the presence of the influence of human activities (Fig. 13), the current centroid coordinates of *Rhodiola kirilowii* were 97.02361°E, 31.71007°N. In the 2050s, under all SSP climate scenarios, the centroid of *Rhodiola kirilowii* migrated northwestward. For example, under the SSP126 scenario, the centroid migrated 156.23 km northwestward, reaching coordinates 95.44471°E, 32.12428°N. In the 2070s, the migration direction remained primarily northwestward: under SSP126 and SSP245 scenarios, the centroid continued to migrate northwestward (e.g., SSP126 migrated 20.85 km to 95.26880°E, 32.23824°N; SSP245 migrated 38.39 km to 94.88538°E, 32.23862°N). Under the SSP585 scenario, the centroid migrated 6.18 km northward, reaching 94.94148°E, 32.18020°N.

Comparing the centroid migration results under both scenarios, the most significant finding is that human activities substantially reduced the distance of centroid migration (e.g., under the SSP126 scenario, in the 2050s, migration was 472.77 km without human activity, but only 156.23 km with human activity). This suggests that human-modified landscapes act as geographical barriers, impeding the species' ability to track its climatically optimal conditions, potentially leading to maladaptation

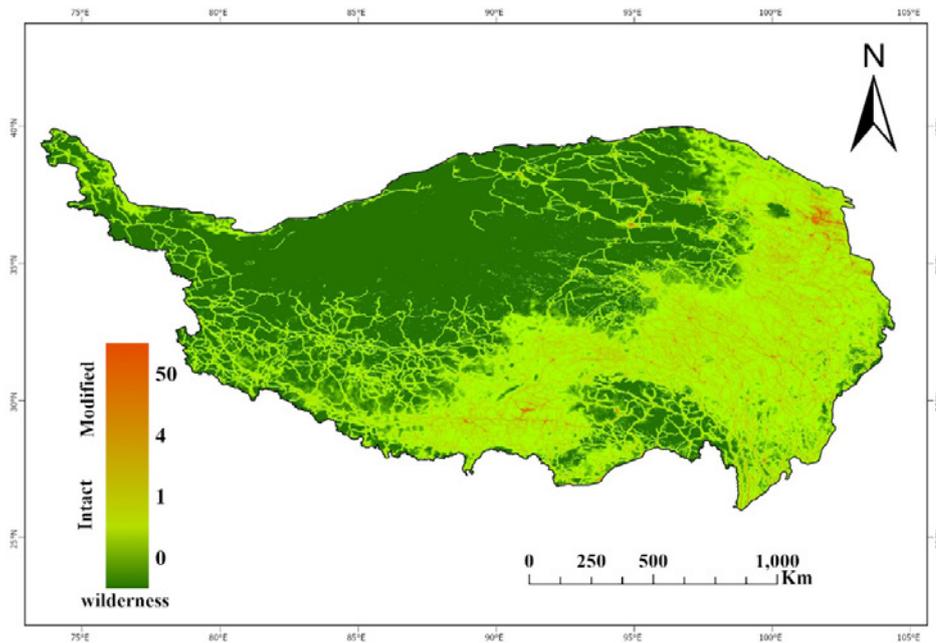


Fig. 14. 2022 Human footprint.

or increased extinction risk. Furthermore, in the 2070s without human activity, the inconsistency in migration direction across different SSP scenarios (northward versus southeastward) indicates that the species' response to climate change may be complex and non-linear. This challenges the simplified assumption that species will consistently migrate poleward or to higher elevations, implying that under more extreme warming, initially suitable areas might become unfavorable, forcing species to shift in unexpected directions. This has profound implications for designing robust, long-term conservation corridors.

Human Activities Dominate the Distribution of Suitable Habitats for *Rhodiola kirilowii*

Generally, plant growth is directly controlled by climate [45]. However, due to its high altitude, low temperatures, and arid environment, the Tibetan Plateau ecosystem is highly sensitive and vulnerable to human activities [46]. Meanwhile, rapid changes in human footprint and land use and land cover change have led to varying degrees of habitat quality degradation [47] and increased habitat fragmentation [48]. A study found that urban expansion in the Pearl River Delta from 2000 to 2020 resulted in decreased habitat quality and deterioration of ecological structure and function [47]. Tang et al. reported a 14.5% decline in total habitat quality in Northeast China, while the area of high habitat degradation levels increased by 2.5%. As the human footprint index rose, the area of high-quality habitat patches decreased by 12.2%, with a significant increase in the proportion of low-quality habitat [49]. Furthermore, Jin et al. found that large anthropogenic infrastructure can increase plant genetic differentiation

within just six years, potentially leading to elevated levels of inbreeding and genetic drift [50]. These findings demonstrate that human-induced habitat fragmentation significantly influences species distribution. High-intensity human activities, such as overgrazing, exert tremendous pressure on local grassland ecosystems, pressure that may far exceed the impacts of climate change [45]. Dong et al. found that local herders and immigrant populations often overlook the carrying capacity of specific pastures, leading to overexploitation of alpine meadows and grasslands and accelerating their overall degradation [51]. Wei et al. also observed reduced vegetation coverage in densely populated and grazing areas [45]. Simultaneously, animal distributions are influenced by human activities. Hua et al. found that the distribution of plateau pikas is correlated with human activity intensity, with high-intensity human activities enhancing their habitat suitability [52, 53]. Therefore, the impact of human activities must be considered in species distribution modeling. A comparison of current suitable habitats reveals significant differences between scenarios with and without human activities. Under human influence, the suitable habitat area for *Rhodiola kirilowii* is substantially reduced, demonstrating the profound effect of human activities on its distribution. Moreover, most alpine plants are incapable of long-distance dispersal [54], which contradicts the extensive northwestward expansion observed in simulations without human activities (Figs. 10 and 12), further underscoring the necessity of incorporating human activities into research. The results of this study indicate that human activities have led to a substantial reduction in the suitable habitat area of *Rhodiola kirilowii*, accompanied by significant fragmentation (Figs. 8 and 9). Furthermore, a large proportion of medium-suitability

habitats for *R. kirilowii* are distributed in regions experiencing moderate human activity intensity (Figs. 8 and 14). The research by Chai et al. [55] demonstrated an increasing trend in NDVI on the Tibetan Plateau from 2000 to 2018 under human influence. Additionally, the impact of human activities on vegetation coverage varies across different regions of the plateau. For instance, vegetation changes in Haibei Prefecture and Changdu City are primarily driven by grazing intensity, while urbanization is the dominant factor in Hainan Prefecture. These findings highlight the dual effects of human activities on plant distribution. Simultaneously, the concentrated distribution of high-suitability habitats for *Rhodiola kirilowii* shifted from the border between Aba Prefecture and Gannan Prefecture to Xining City. This shift may be attributed to Xining's climatic conditions, ecological conservation projects, and concentrated cultivation bases. Investigations show that Xining has an average annual temperature of -6.7°C to 6.8°C and an annual precipitation of 353-590 mm [56], which aligns broadly with the findings of this study. According to Hong et al. [57], the Sichuan Academy of Grassland Sciences established a desertification control demonstration base in Hongyuan County, Aba Tibetan and Qiang Autonomous Prefecture, Sichuan Province, where *R. kirilowii* and sea buckthorn were planted for sand fixation, thereby increasing the distribution area of *R. kirilowii*.

Areas with significant human activity intensity on the Tibetan Plateau are primarily distributed in its eastern and central-southern regions (Fig. 14), forming a roughly belt-shaped spatial pattern extending from Rigaze-Lasa-Naqu-Yushu-Goluo-Xining. High-intensity areas primarily consist of the Lhasa urban area, centered around Chengguan District, Doilungdêqên District, and Dagzê District of Lhasa City, and the Xining urban area, centered around Xining City and Haidong City. These two regions represent the primary population centers and urbanization development zones on the Tibetan Plateau [58], and are characterized by human activities manifested through a high proportion of construction land, intense nighttime light intensity, and dense road networks [36]. Medium-intensity areas are relatively evenly distributed along the borders of Qinghai, Gansu, Sichuan, and Tibet. Human activities in these regions are primarily characterized by agricultural development and grazing practices [58]. Disturbances from grazing activities, combined with habitat fragmentation caused by construction projects and highways on the Tibetan Plateau, have led to the degradation of grassland ecosystems, resulting in a reduction of suitable habitats for *Rhodiola kirilowii* [58, 59]. The disappearance of large areas of high and medium-suitability habitats for *Rhodiola kirilowii* in Aba, Ganzi, and Gannan Prefectures may be attributed to disordered exploitation and unsustainable utilization of *Rhodiola* resources on the Tibetan Plateau. Harvesting methods commonly involve uprooting whole plants, and in some regions, even burning flowering stems, which severely damage

the habitats of *Rhodiola* species [22]. Investigations by Brinckmann et al. [60] revealed chaotic acquisition practices and excessive harvesting of medicinal *Rhodiola*, leading to rapid resource depletion and a sharp decline in suitable habitat areas.

Main Driving Factors Influencing the Potential Distribution of *Rhodiola kirilowii*

Given the significant impact of human activities on plant distribution, this section focuses exclusively on simulation scenarios incorporating human influences. Under the influence of human activities, the structure of dominant factors shifts, with human activities becoming the primary driver. Human activities exhibit a dual impact on plant distribution: ecological efforts, soil-water conservation measures, and wildlife protection promote vegetation growth, whereas overgrazing, urbanization, and construction land expansion contribute to habitat fragmentation and loss [61-64]. This study reveals that the optimal elevation range under human influence is 4000-5000 m, likely due to the upward shift of *Rhodiola kirilowii*'s suitable habitats to higher altitudes in response to human pressures in lower-elevation regions of the Tibetan Plateau [58]. Furthermore, He et al. [65] observed a significant wetting trend in northwestern China from 1961 to 2014 under human influence, with prolonged rainy seasons and intensified future precipitation seasonality, consistent with the findings of this study.

Changes in *Rhodiola kirilowii* Suitable Habitat under Future Climate Change

Liu et al. found that climate change promotes vegetation growth [66], which aligns with the results of this study. Regardless of human activities, the future suitable habitats of *Rhodiola kirilowii* exhibit an expanding trend; therefore, this section focuses solely on the impact of climate change on its distribution. Currently, global climate change is reshaping the terrestrial ecosystem patterns of the Tibetan Plateau at an unprecedented rate. Since the 1970s, the global surface temperature has been rising at a rate of 0.2°C per decade, directly causing latitudinal or elevational shifts in the distribution ranges of over 50% of plant species [54]. This is consistent with the findings of the present study, which also indicates that, in the absence of human activities, *R. kirilowii* exhibits even longer migration distances.

Temperature and precipitation on the Tibetan Plateau show significant spatial heterogeneity, increasing from northwest to southeast [67]. *R. kirilowii* thrives in sunny, warm, and humid climatic conditions. The southeastern regions (e.g., Sichuan, Yunnan, and Qinghai provinces) offer suitable climates with ample precipitation and relatively humid air, meeting the growth requirements of *R. kirilowii*. Consequently, its suitable habitats are

primarily distributed in the eastern part of the Tibetan Plateau (Figs. 8 and 9).

In response to climate change, species adaptation strategies typically involve dispersal to new suitable areas or extinction, in addition to physiological adjustments [68]. The trend toward warmer and wetter climatic conditions impacts the growth and physiological processes of *Rhodiola kirilowii* [4, 34]. The species' response to climate change is primarily reflected in the extent, quality, and spatial distribution of its suitable habitats. Under the SSP126, SSP245, and SSP585 scenarios for the 2050s and 2070s, the suitable habitat area for *R. kirilowii* on the Tibetan Plateau expands significantly, with a greater increase observed in the 2050s compared to the 2070s. This study identifies temperature, precipitation, and human activities as the main factors influencing the distribution of suitable habitats for *R. kirilowii*. Umair et al. [69] found that temperature and precipitation on the Tibetan Plateau exhibit a significant negative correlation with elevation. Additionally, regional variations in precipitation occur due to the combined influences of westerly winds and the Indian monsoon [67]. Hu et al. [5] projected future climate conditions on the Tibetan Plateau under the RCP4.5 moderate-low radiative forcing scenario, indicating a temperature increase proportional to elevation, along with rising annual and seasonal precipitation. These changes suggest that the future climate of the Tibetan Plateau will become increasingly suitable for *Rhodiola kirilowii*, resulting in a significant expansion of its suitable habitat. The results of this study show that the suitable habitat area for *R. kirilowii* first increases substantially and then slightly decreases under climate change, indicating that future climatic conditions will initially favor its survival, followed by a recoverable reduction. This pattern may arise from ongoing climate changes, to which *R. kirilowii* gradually adapts while maintaining population stability, thereby sustaining a dynamic equilibrium in suitable habitat area.

Under the three climate scenarios, the medium and high suitability habitats for *Rhodiola kirilowii* in the 2050s and 2070s not only expanded in area but also increasingly clustered within 32°0'-36°0'N and 102°0'-104°0'E, with a more uniform distribution. The predictions of this study indicate that the suitable elevation range for *R. kirilowii* is 3300-3800 m, while under human influence, it shifts to 4000-5000 m. Compared to *Rhodiola crenulata* and *Rhodiola tangutica*, *R. kirilowii* exhibits a narrower suitable elevation range. This may be attributed to the limited number of spatially filtered occurrence points available for *R. kirilowii*, combined with challenges in field surveys, such as inaccessible high-altitude locations due to harsh climate conditions and the high cost of unbiased sampling, resulting in insufficient data from the central and western Tibetan Plateau and ultimately leading to a narrower predicted distribution range.

Centroid Migration Analysis

Parmesan and Yohe [70], through an integration of global species distribution data, found that 80% of species exhibited poleward or upward shifts in response to climate warming. This study observed a northwestward migration of *Rhodiola kirilowii*, which may be related to the unique growth environment of Tibetan medicinal *Rhodiola* species. These plants primarily inhabit high-altitude alpine environments, and the eastern and southern Tibetan Plateau, characterized by steep altitudinal gradients and numerous peaks [34], may facilitate upward migration of mountain plants [71]. Future increases in temperature and precipitation on the Tibetan Plateau could make northwestern regions more suitable for *R. kirilowii* [5]. Additionally, human activities may influence the climate of the Tibetan Plateau [72], potentially shortening the migration distance of *R. kirilowii*. Given the complex topography, significant regional elevation variations, and rapid climate change on the Tibetan Plateau [64], further consideration is needed to assess whether newly emerging suitable habitats under future climate conditions will be accessible for species migration.

Furthermore, studies have indicated that factors such as invasive species and community structure can also influence species distributions to varying degrees [73]. Invasive plants pose serious threats to the survival and distribution of native species through resource competition, allelopathy, and alteration of ecosystem processes [74-76]. For instance, *Solidago canadensis* suppresses the growth of neighboring plants via intense root competition and allelopathic effects, demonstrating greater tolerance to interspecific competition than the native species *Imperata cylindrica* [74]. *Sonneratia apetala* Buch.-Ham., a classic example of a species introduced through restoration projects that later became invasive, grows rapidly and forms a dense canopy. This shading deprives understory native mangrove seedlings (e.g., *Aegiceras corniculatum*, *Avicennia marina*) of essential light, thereby displacing and replacing native species [75]. Such biotic factors are often simplified or omitted in current species distribution models, which may lead to an optimistic bias in predictions of future potential distributions. In subsequent research, variable selection should consider the correlation between species' growth habits and environmental factors. By comprehensively integrating environmental variables affecting species distribution, a more holistic set of factors can be identified to improve the accuracy of model predictions.

Conclusions

Based on 123 distribution records from the Tibetan Plateau and 32 environmental variables, this study employed an optimized MaxEnt model to predict the potential geographical distribution of *Rhodiola kirilowii*

on the Tibetan Plateau. Under climate change scenarios, human activities significantly influence the distribution of suitable habitats for *R. kirilowii* and represent a key constraint on its distribution. Currently, *R. kirilowii* is primarily distributed in the border regions of Qinghai, Gansu, Sichuan, Yunnan, and Tibet. Under human activities, the suitable habitat area for *Rhodiola kirilowii* decreased significantly by 47.67%. In the future, regardless of human influence, the suitable habitat area is projected to expand, with the distribution center shifting toward the northwestern Tibetan Plateau. Thus, human activities profoundly affect the distribution of *R. kirilowii*, necessitating further research in this area. The protection and sustainable use of *R. kirilowii* resources are urgently needed. Targeted measures must be implemented to conserve existing wild resources while mitigating the impact of human activities. Additionally, associated plant species may influence the growth and distribution of *R. kirilowii*, though current understanding remains limited. Further in-depth studies are required to comprehensively elucidate the factors affecting its suitable habitats. For other species within the *Rhodiola* genus, there is an urgent need to investigate their current status and future trends to provide a scientific basis for germplasm conservation, field protection, cultivation, and domestication of Tibetan medicinal species.

Author Contributions

T.-Y.Y., J.-M.Y., and K.Y. planned and supervised the project. H.-K.L. and T.-H.Z. performed the experiments, analyzed the data, contributed reagents/materials/analysis tools. R.-T.H. and B.-G.M. contributed to data collection and evaluation. J.Y., T.-Y.Y., and Y.H. revised the manuscript.

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Conflict of Interest

The authors declare no conflict of interest.

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