

# Global temporal distribution of Maca (*Lepidium meyenii* Walp.) under climate change

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## Research Article

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# Abstract

Global warming has influenced phenological shifts and community degradation in alpine herbaceous plants. However, the current distribution and future shifts of these plants and their environmental driving factors under climate change are not well known. Here, we focus on *Lepidium meyenii*, a medicinal herb native to the high-altitude regions of the Andes Mountains in South America, which may face habitat contraction and potential population decline in the future due to changing environmental conditions. We integrate species distribution data with a random forest model to simulate the potential habitats of *L. meyenii* across time and identify their key environmental drivers. We find that the most significant environmental variables that impact the distribution of *L. meyenii* include elevation, temperature annual range (bio7), and mean diurnal range (bio2). Since the Last Glacial Maximum, the western Andes in South America has consistently offered suitable habitat for *L. meyenii*. In contrast, habitat suitability in the Tibetan Plateau (TP) has varied over time, and in the future the TP may become a potential area for biodiversity conservation. This study will enhance our understanding of the distribution patterns of alpine herbaceous plants in response to climate change, and contributes to future biodiversity conservation efforts, the establishment of protected areas, and the sustainable management of medicinal plants as biological resources.

## 1. Introduction

Since the Industrial Revolution, the surge in greenhouse gas emissions resulting from industrialization has led to a rise in global average temperatures by 0.5 °C. It is projected that by 2100, under moderate and high emissions scenarios (SSP2-4.5 and SSP5-8.5), global temperatures will increase by 2.3–4.6 °C and 6.6–14.1 °C, respectively, compared to pre-industrial levels [1, 2]. Climate change not only alters weather patterns but also exacerbates the frequency and severity of extreme climatic events, such as heavy rainstorms, droughts, and storms [3]. As a major consequence of global warming, climate change is increasingly recognized as a key driver of species distribution shifts [4, 5, 6]. Many species are moving to higher altitudes and latitudes as temperatures rise [4, 7]. These shifts not only change distribution patterns but also have significant implications for biodiversity and ecosystems [8, 9]. Furthermore, species niche shifts occur at a much slower rate than the pace of climate change [10]. This highlights potential risks of habitat mismatch and biodiversity loss. Therefore, it is essential to understand the relationship between climate change and species distribution for developing effective conservation strategies.

Species distribution models (SDMs) are developed to investigate the relationship between climate change and species distribution. They analyze the interactions between species and environmental variables to predict potentially suitable distributions. SDMs also incorporate the physiological responses and adaptation mechanisms of species [11]. Common algorithms used in species distribution modelling include the maximum entropy model (MaxEnt) [12], random forest (RF) [13], generalized additive model (GAM) [14] generalized linear model (GLM) [15], among others. The biomod2 package in R is widely adopted for species distribution modelling [16, 17]. It integrates various algorithms and allows users to

customize parameters for different applications [18]. Selecting the optimal model is important for accurately predicting potentially suitable areas for species, and this can be achieved through the quantitative evaluation of different SDMs. Among these algorithms, the MaxEnt model, when parameter-tuned using the ENMeval R package, is particularly popular. It effectively reduces overfitting compared to default settings and significantly improves predictive performance [19].

*Lepidium* L. is a genus within the Brassicaceae family, and comprises 265 species (<https://www.powo.science.kew.org>). It is widely distributed across all continents except Antarctica and can be found in high-altitude regions [20, 21]. The genus originated in Eurasia, evolved, and thrived in the Mediterranean region before its long-distance dispersal to the Americas and Australia during the late Neogene or Quaternary periods [22, 23]. *L. meyenii* is an alpine herbaceous species native to the Andean region of western South America. It diverged ca. 12 million years ago [24], and has adapted to the extreme conditions of high altitudes. It is commonly referred to as "Peruvian ginseng" and possesses significant economic value due to its rich nutrient profile and numerous health benefit, including enhancing fertility, reducing fatigue, balancing hormone levels, and improving athletic performance [25, 26, 27, 28, 29, 30]. Consequently, products derived from *L. meyenii* have gained considerable market popularity [31]. Since the 1990s, cultivation attempts in the United States, Japan, and Germany have met with limited success, while China successfully domesticated *L. meyenii* in 2002 and has established a substantial market. For example, in Yunnan Province, the cultivation area of *L. meyenii* has reached 22,000 hm<sup>2</sup> [32, 33].

Climate change can lead to alpine gravelization and thus result in the degradation of meadow communities [34], and significantly affect the phenology of alpine herbaceous species [35]. The ecological adaptation mechanism of *L. meyenii* may change in response to global warming which could impact its distribution. Therefore, it is crucial to investigate the changes in the distribution patterns of *L. meyenii* under future climate change scenarios to develop effective cultivation strategies that ensure its sustainable development and conservation.

In this study, we address the following questions: 1) What are the critical environmental variables that influence the distribution of *L. meyenii*? 2) How has the suitable habitat for *L. meyenii* changed from the past to the present? 3) How will *L. meyenii* respond to future climate change? To answer these questions, we quantitatively compare the MaxEnt model, optimized with the ENMeval package, against 10 other models from the biomod2 package to simulate the potential suitable areas for *L. meyenii* under various climatic conditions across different time periods. We aim to reconstruct the past, present, and future potential suitable areas for *L. meyenii*, understand the key environmental factors that drive its distribution, and provide new insights for the conservation and sustainable development of herbaceous plants in the context of global climate change.

## 2. Data and Methods

### 2.1 Natural distribution area—western North America

*L. meyenii* is primarily distributed along the western coast of South America within the Andes, encompassing parts of northwestern Argentina, Bolivia, Peru, and the western region of Brazil (Fig. 1). The Andes Mountain Range stretches from north to south, with its average elevation that decreasing and then increasing along its length. Within the latitudinal range of 10–30° S, the average altitude is ca. 3000 m, which coincides with the area where *L. meyenii* is most densely populated [36]. The climate in western South America is highly complex, shaped by the perennial effects of the Peru Current, the barrier created by the Andes, and the South American monsoon system. These factors contribute to a diverse range of climates from north to south, including tropical arid, tropical humid, savanna, semi-arid, and temperate oceanic climates [37, 38, 39].

## 2.2 Species distribution and climate data, and environmental variables

The present-day distribution data for *L. meyenii* were obtained from the Global Biodiversity Information Facility (<http://www.gbif.org>; GBIF.org, 2025) and subsequently cleaned [40]. We first used ENMTools to eliminate duplicate coordinates and performed random gridding, ensuring that only one occurrence per 5' × 5' grid cell was retained. We then applied the “clean\_coordinates” function from the “CoordinateCleaner” R package v3.0.1 [41] to exclude records with potentially erroneous geographical coordinates. Based on previous studies and information from Plants of the World Online (<https://www.powo.science.kew.org>), we confirmed that *L. meyenii* is native only to northwestern Argentina, Bolivia, northern Chile, and Peru, thus excluded all records outside these regions [42, 43]. We eventually obtained 64 valid natural distribution records for *L. meyenii*.

We selected 22 environmental variables from the WorldClim database (<http://worldclim.org>), including 19 bioclimatic and 3 topographic variables (Table S1). The bioclimatic variables for these periods were chosen at a spatial resolution of 5' (ca. 85 km<sup>2</sup>). Present-day climate data represent average conditions from 1970 to 2020, while past and future climate data were derived from various global climate models (GCMs).

We simulated the potential distributions of *L. meyenii* for the past (Last Glacial Maximum—LGM, ca. 22,000 years ago; Mid-Holocene—MH, ca. 6000 years ago), present, and future (for 2050 and 2090, representing averages from 2040–2060 and 2080–2100, respectively). Averages of climate data for the LGM were obtained from three available GCMs (CCSM4, MIROC-ESM, and MPI-ESM-P), while averages for the MH were obtained from nine GCMs (BCC-CSM1-1, CCSM4, CNRM-CM5, HadGEM2-CC, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM, MPI-ESM-P, and MRI-CGCM3) in WorldClim v1.4. Future climate data were averaged from three GCMs (FIO-ESM-2-0, MPI-ESM1-2-HR, and MRI-ESM2-0), which performed better than other models across different regions [44].

The two future periods were chosen to illustrate both short-term and long-term trends in habitat changes. For each period, we incorporated two climate scenarios from CMIP6 GCM: SSP245 (a moderate-emission scenario) and SSP585 (a high-emission and pessimistic scenario) [45]. To minimize the impact of multicollinearity among environmental variables on model accuracy and to prevent

overfitting, we conducted a Pearson correlation analysis using ENMTools software. Subsequently, we excluded highly correlated variables ( $|r| < 0.8$ ), and selected ten environmental variables for simulation: annual mean temperature (bio1), mean diurnal range (bio2), temperature annual range (bio7), annual precipitation (bio12), precipitation of driest month (bio14), precipitation seasonality (bio15), precipitation of coldest quarter (bio19), aspect, slope and elevation (Fig. S1).

## 2.3 Model selection

We employed both ENMeval and biomod2 packages for model analysis [18, 19]. All environmental variable data were converted to ASCII format using ArcGIS 10.8.1. The ENMeval package was utilized to optimize MaxEnt model parameters [19], enabling us to test various feature combination (FC) and regularization multiplier (RM) to identify the most suitable settings. The MaxEnt software offers five types of FC: L (linear), Q (quadratic), H (hinge), P (product), and T (threshold). To refine the model, we tested RM values from 0.5 to 6 in increments of 0.5, resulting in a total of 12 RM values. Additionally, we evaluated six different FC combinations: L, LQ, H, LQH, LQHP, and LQHPT. In total, we assessed 72 parameter combinations using the corrected Akaike Information Criterion (AICc), selecting the configuration with the lowest AICc value to ensure an optimal balance between model fit and complexity. A model is considered optimal when  $\Delta AICc = 0$ . The best-performing configuration is FC = LQHP and RM = 3, with  $\Delta AICc = 0$  (Table S2).

We then used the biomod2 package to construct models with 11 different algorithms for simulations: artificial neural network (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multivariate adaptive regression splines (MARS), maximum entropy model (MaxEnt), random forest (RF), surface range envelope (SRE), and extreme gradient boosting (XGBoost). The optimized MaxEnt model parameters from the previous step were implemented in biomod2, while all other models were executed with their default settings. To minimize model uncertainty, the dataset was randomly partitioned into a training set (75%) and a testing set (25%), with each model repeated 20 times. Following the recommendations of the biomod2 team, we generated 200 pseudo-absence (PA) points, which is three times the number of occurrence points [46].

Finally, the selection of the best-performing model was based on the receiver operating characteristic (ROC) and true skill statistics (TSS) [47, 48, 49]. We analyzed the area under the curve (AUC) and TSS values to compare the performance of 11 models in simulating the potential suitable habitats for *L. meyenii*. Model performance was evaluated with the following criteria: (1) poor ( $AUC < 0.6$ ), (2) fair ( $0.6 \leq AUC < 0.8$ ), (3) good ( $0.8 \leq AUC < 0.9$ ), and (4) excellent ( $0.9 \leq AUC < 1$ ) [50, 51]. Additionally, a TSS value greater than 0.8 is generally considered indicative of excellent model performance [52].

## 2.4 Classification of habitat suitability and centroid analysis of suitable areas

We applied the natural breaks method in ArcGIS 10.8.1 to classify habitat suitability into four categories: 0–0.2 (suitable), 0.2–0.4 (lowly suitable), 0.4–0.6 (moderately suitable), and 0.6–1 (highly suitable) [5]. These categories were subsequently reclassified as follows: 0–0.2 = 0, 0.2–0.4 = 1, 0.4–0.6 = 2, and 0.6–1 = 4. Raster calculations were performed by subtracting suitability maps of earlier periods from those of later periods, where values < 0, = 0, and > 0 indicate areas of contraction, unchange, and expansion, respectively. This analysis provides insights into the temporal dynamics of potentially suitable distribution areas for *L. meyenii*.

Using the centroid calculation function in ArcGIS 10.8.1, we also calculated the areas of habitat suitability classified as moderate or higher and identified the centroids of potentially suitable habitats for *L. meyenii* across three time periods: the past, the present and the future in both South America and East Asia. This analysis enables us to track shifts in the centroids of suitable habitats for *L. meyenii* over time in response to climate change. By examining these centroid movements, we can understand how favorable growing conditions for *L. meyenii* have geographically relocated as a result of changing climatic factors.

### 3. Results

#### 3.1 The random forest (RF) has the optimal performance

Based on the AUC and TSS values, and the actual simulation outcomes, the random forest (RF) model shows the best performance, with an AUC of 0.9888 and a TSS of 0.8726 (Fig. 2). These metrics demonstrate its superior accuracy in predicting the distribution of suitable habitats for *L. meyenii*.

#### 3.2 Elevation and temperature annual range (bio7) are the most critical factors

The present-day distribution of *L. meyenii* is shaped by both climatic and topographic factors (Fig. 3). The most significant environmental variables influencing this distribution are elevation (47.6%), temperature annual range (bio7) (24.1%), mean diurnal range (bio2) (10.4%), slope (8.6%), annual mean temperature (bio1) (4.4%), precipitation seasonality (bio15) (2.2%), precipitation of coldest quarter (bio19) (1%), annual precipitation (bio12) (0.8%), precipitation of driest month (bio14) (0.7%), and aspect (0.2%) (Fig. 3). Consequently, elevation and the temperature annual range (bio7) emerge as the most critical factors that influence the current distribution of *L. meyenii*.

The probability of occurrence for *L. meyenii* shows a positive correlation with elevation, bio2, and slope. Specifically, *L. meyenii* thrives at elevations above 2000 m, where the mean diurnal range exceeds 13 °C, and slopes are greater than 1°. Conversely, the probability of occurrence is negatively correlated with temperature annual range (bio7). This indicates that *L. meyenii* grows better when temperature annual range is less than 20 °C.

### 3.3 Potential distribution under past, current, and future climate conditions

The simulation results suggest that highly suitable areas are predominantly concentrated in the Andes Mountains of western South America, consistent with current sampling locations, while moderately suitable areas are mainly found in the Tibetan Plateau, and lowly suitable areas are more widely dispersed (Fig. 5). Specifically, suitable habitats in the Tibetan Plateau have undergone significant changes through time: 1) During the LGM and MH, the habitat was predominantly of moderate suitability; 2) At present and in 2050 (under the SSP245 scenario), moderately and lowly suitable areas are interspersed; and 3) By 2050 (SSP585) and 2090 (for both SSP245 and SSP585), a larger area classified as highly suitable appears along the southern edge of the Tibetan Plateau. This reaches its maximum extent in 2090 under the SSP585 scenario.

During the LGM, the total area of potential suitable habitat was  $1190.5 \times 10^4 \text{ km}^2$ , the largest among all time periods, although it had the smallest highly suitable area, covering only  $68.3 \times 10^4 \text{ km}^2$ . From the past to present, the total suitable habitat has decreased by ca. 12%. From the present to 2090 under the SSP245 scenario, the total suitable habitat area will decrease from  $1047.5 \times 10^4 \text{ km}^2$  to  $976.1 \times 10^4 \text{ km}^2$ , with a reduction of 6.81%. However, the highly suitable area is projected to decline from  $70.0 \times 10^4 \text{ km}^2$  to  $74.3 \times 10^4 \text{ km}^2$ , with an increase of 6.1%, while the moderately suitable area will rise from  $170.0 \times 10^4 \text{ km}^2$  to  $171.2 \times 10^4 \text{ km}^2$ , with an increase of 0.72%. In comparison, from the present to 2090 under the SSP585 scenario, the total suitable habitat area will decrease significantly to  $957.4 \times 10^4 \text{ km}^2$ , with a decline of 8.6%. In contrast, both the highly suitable and moderately suitable areas are projected to increase substantially, which reach  $78.3 \times 10^4 \text{ km}^2$  with an increase of 11.75% and  $174.7 \times 10^4 \text{ km}^2$  with an increase of 2.01%, respectively.

Table 1  
Temporal changes in the area ( $10^4 \text{ km}^2$ ) of suitable habitats for *Lepidium meyenii*.  
Abbreviations: LGM = Last Glacial Maximum, MH = Mid-Holocene.

| Period        | Lowly suitable | Moderately suitable | Highly suitable | Total  |
|---------------|----------------|---------------------|-----------------|--------|
| LGM           | 895.7          | 226.5               | 68.3            | 1190.5 |
| MH            | 768.0          | 231.7               | 77.9            | 1078.6 |
| Present       | 807.4          | 170.0               | 70.0            | 1047.5 |
| SSP245 (2050) | 742.5          | 168.2               | 72.7            | 983.3  |
| SSP585 (2050) | 726.1          | 163.8               | 75.5            | 965.3  |
| SSP245 (2090) | 730.6          | 171.2               | 74.3            | 976.1  |
| SSP585 (2090) | 704.4          | 174.7               | 78.3            | 957.4  |

### 3.4 Changes in potential habitat suitability since the LGM

Generally, both historical data and future projections indicate that the area of habitat contraction for *L. meyenii* globally exceeds the area of habitat expansion. Additionally, the extent of both habitat expansion and contraction was more pronounced in the past (Fig. 6, Table 2). Between the LGM and the MH, as well as from the MH to the present, an opposing trend emerged in the areas with expansion and contraction across South America, Africa, and East Asia. Specifically, from the LGM to the MH, the global potential suitable habitat contracted by  $346 \times 10^4 \text{ km}^2$  mainly in southern and eastern Africa, and expanded by  $260.6 \times 10^4 \text{ km}^2$  primarily along the edges of the Tibetan Plateau, Southeast Asia, and northern South America. From the MH to the present, the global potential suitable habitat contracted by  $312.5 \times 10^4 \text{ km}^2$  mainly in the Tibetan Plateau and northern South America, with an expansion of  $204 \times 10^4 \text{ km}^2$  distributed without significant concentration.

In the future, habitat contraction is expected primarily along the southern edge of the Tibetan Plateau, with additional scattered regions of contraction in southern Africa and northwestern China. Under the SSP245 scenario, changes in suitable habitats for *L. meyenii* are moderate. By 2050, the area of contraction is projected to be  $126.7 \times 10^4 \text{ km}^2$ , while the area undergoing expansion is estimated at  $71.8 \times 10^4 \text{ km}^2$ ; in 2090, these areas are expected to increase to  $149.2 \times 10^4 \text{ km}^2$  and  $93.5 \times 10^4 \text{ km}^2$ , respectively. In contrast, under the SSP585 scenario, changes in suitable habitats for *L. meyenii* are expected to be more pronounced. By 2050, the areas with contraction and expansion will be  $152.6 \times 10^4 \text{ km}^2$  and  $80.7 \times 10^4 \text{ km}^2$ ; By 2090, these areas are projected to expand further to  $210.9 \times 10^4 \text{ km}^2$  for contraction and  $147.7 \times 10^4 \text{ km}^2$  for expansion.

Table 2

Temporal changes in the distribution area ( $10^4 \text{ km}^2$ ) for *Lepidium meyenii*.  
LGM = Last Glacial Maximum, MH = Mid-Holocene.

| Period                      | Unchanged | Contracted | Expanded |
|-----------------------------|-----------|------------|----------|
| LGM–MH                      | 12887.4   | 346.0      | 260.6    |
| MH–Present                  | 12977.5   | 312.5      | 204.0    |
| Present–SSP245 (2050)       | 13295.5   | 126.7      | 71.8     |
| SSP245 (2050)–SSP245 (2090) | 13251.3   | 149.2      | 93.5     |
| Present–SSP585 (2050)       | 13260.8   | 152.6      | 80.7     |
| SSP585 (2050)–SSP585 (2090) | 13135.3   | 210.9      | 147.7    |

### 3.5 Temporal centroid migration of potential suitable areas for *L. meyenii*

The migration trend is more pronounced in the past compare to the future. In South America, the centroid of suitable habitats for *L. meyenii* generally shifts northward over time (Fig. 7a). From the LGM to the MH, the centroid moves north by 135 km, from coordinates 9.71° S, 67.44° W to 8.49° S, 67.41° W.

By the present day, it has further shifted 50.8 km to 8.03° S, 67.35° W. Under the SSP245 scenario, the centroid migrates northwest by 28.3 km to 7.87° S, 67.55° W by 2050, and then further to 7.35° S, 67.47° W, with a total movement of 58.1 km by 2090. In the SSP585 scenario, the centroid is expected to move to 7.73° S, 67.48° W by 2050, with a shift of 35.8 km, and then slightly to 7.66° S, 67.44° W by 2090, with a distance of 9.6 km.

In East Asia, the centroid migration generally follows an initial southeastward to westward trend (Fig. 7b). From the LGM to the MH, the centroid shifts southeast by 252.8 km from 34.03° N, 93.93° E to 31.96° N, 95.12° E. By the present day, it has moved west to 32.19° N, 92.68° E with 231.9 km. Under the SSP245 scenario, the centroid shifts with 61.3 km further west to 32.11° N, 92.03° E by 2050, and then to 32.33° N, 92.34° E by 2090, with a further movement of 38.1 km. In the SSP585 scenario, the centroid moves to 32° N, 92.25° E with 45 km, then to 32.45° N, 92.57° E with 56 km.

## 4. Discussion

### 4.1 The evaluation of model performance

We optimized the MaxEnt model with the ENMeval package and compared it with other models available in the biomod2 package. The results indicate that the random forest (RF) model outperforms others in simulating the potential suitable habitats of *L. meyenii* through time. The optimized MaxEnt model shows a significant improvement over the default parameters, with an increase of 0.08 in AUC and 0.05 in TSS, though its accuracy remained lower than that of the RF model.

As an ensemble learning method based on the CART model, RF is widely used in ecology and biogeography due to its stability, insensitivity to parameter tuning, and ability to maintain high accuracy even with small sample sizes [53, 54]. While the RF model showed superior performance in this study, the best model may differ among various species. Many studies have opted for ensemble models in biomod2 to overcome the limitations of single models [55, 56]. However, ensemble models do not always outperform an individual model, as an optimized single model can sometimes provide better predictive performance [57]. Therefore, we emphasize the importance of an integrative evaluation of different models with quantitative methods to identify the optimal model and ensure the accuracy and robustness of the simulation results.

### 4.2 Key environmental variables and potential distribution in the present day

The most critical factors that influence the potential suitable habitat distribution of *L. meyenii* are elevation, temperature annual range (bio7), mean diurnal range (bio2), and slope (Figs. 3, 4). Elevation and slope are topographic variables, while bio7 and bio2 relate to temperature. Precipitation has a minor role in determining species distribution. *L. meyenii* is primarily found in areas with elevations exceeding 2,000 m, a mean diurnal temperature range over 15°C, and an annual temperature range below 20°C

(Fig. 4). This suggests that the species is better adapted to high-altitude environments characterized by significant diurnal temperature variations and relatively low annual temperature fluctuations.

The Andes Mountains in western South America represent the largest area of natural distribution for plants, while Yunnan in China is known for the largest area of cultivated introduction [58]. These regions share similar climatic characteristics influenced by monsoonal climates, which promote the growth of *L. meyenii* [59, 60, 61]. Genomic sequencing and analysis of *L. meyenii* reveal its molecular mechanisms that enable its adaptation to extreme high-altitude environments characterized by low temperatures and intense ultraviolet radiation [24]. This study further confirms earlier results. A low annual temperature range provides a relatively stable environment for growth, while a high diurnal temperature range enables plants to optimize daytime photosynthesis and reduce nighttime respiration, and this thereby promotes organic matter accumulation [62]. However, species distribution is influenced not only by climate and topography but also by factors such as sunlight, soil, and water availability [63]. Future studies on *L. meyenii* distribution should incorporate a wider array of environmental variables.

The primary potential suitable habitats for *L. meyenii* at present are located in western South America and the southern edge of the Tibetan Plateau. Both regions feature alpine and plateau climates, are situated in subtropical zones, and have elevations exceeding 2,000 m, along with an annual temperature range below 20°C and a mean diurnal temperature range above 15°C, and this makes them highly conducive to *L. meyenii* growth. This climate type is characterized by low annual temperature variation, significant diurnal temperature fluctuations, strong ultraviolet radiation, low atmospheric pressure, and high wind speeds. The current potential suitable habitats for *L. meyenii* align well with its natural distribution in western South America and its cultivated areas in Yunnan, China (Fig. 3).

## 4.3 Changes in potential suitable habitat from past to present

During the LGM–MH, the contraction of potential suitable habitat for *L. meyenii* predominantly occurred in central South America and eastern and southern Africa (Fig. 6a), while expansion was primarily observed along the edges of the Tibetan Plateau, Southeast Asia, and northern South America. This pattern may be associated with global warming and regional monsoon dynamics during the LGM–MH, as both factors contributed to a decrease in the annual temperature range (bio7). The intensification of the South Asian and East Asian monsoons during this period created a more favorable climatic condition for the survival of *L. meyenii* along the edges of the Tibetan Plateau and in Southeast Asia, and thereby this facilitated the expansion of its suitable habitat range [64, 65].

In the LGM, cooling in the Northern Hemisphere caused a southward shift of the Intertropical Convergence Zone (ITCZ). In contrast, during the MH, the ITCZ shifted northward, and this led to intensified monsoons in northern South America while weakening them in central and southern regions [66, 67]. Consequently, as northern South America experienced significant habitat expansion, central regions saw a greater contraction (Fig. 6a). By the MH, the centroid of the potential suitable habitat shifted northward (Fig. 7a). This suggests that, *L. meyenii* was inclined to expand toward lower latitudes

in South America. During the MH, Africa experienced significantly warmer climatic conditions, which were unfavorable for *L. meyenii*, a cold-adapted alpine herb. This resulted in substantial contractions of suitable habitats in eastern and southern Africa. Similar distribution shifts have been observed in *Xerophyta* species across Africa [68].

From the MH to the present, the contraction of suitable habitat for *L. meyenii* has primarily occurred in the Tibetan Plateau and northern South America, with only limited expansion observed (Fig. 6b). This contraction may be closely related to elevation-dependent warming (EDW)—a phenomenon where high-altitude regions experience more rapid temperature increases compared to low-altitude areas due to greenhouse gas emissions [68]. Both the Tibetan Plateau and the Andes Mountains are affected by EDW, which accelerates climate change in alpine ecosystems and modifies vegetation distribution [69]. This process has led to habitat contraction or shifts, with negative consequences for biodiversity [39].

When comparing the LGM–MH and MH–Present periods, the primary areas with contraction and expansion for *L. meyenii* show opposite patterns, particularly in the Tibetan Plateau and northern-central South America. Similarly, many high-altitude, cold-adapted plant species have undergone comparable distribution shifts during these two periods [70]. We conclude that natural environmental factors primarily drove changes in plant distribution during the LGM–MH, while human activities have increasingly influenced distribution during the MH–present period, particularly under the EDW effect in high-altitude regions. Therefore, future studies should integrate human activities as an environmental variable in distribution models to better understand their impact on shifts in species habitat.

## **4.4 Changes in potential suitable habitat from the present to the future**

In the future, the most significant expansion of suitable habitat for *L. meyenii* is projected to occur along the southern margin of the Tibetan Plateau, while the most substantial contraction is observed in the Tarim Basin of northwestern China and southern Africa. Although the suitable habitat in South America shows minimal overall change, its centroid continues to shift northward. Specifically, in the SSP245 scenario, global average temperatures are anticipated to rise by ca. 2.3–4.6°C above pre-industrial levels, while in the SSP585 scenario, the increase could be 6.6–14.1°C [3]. The Tarim Basin is thought to become even hotter under these future climate conditions [71]. Given its significant diurnal and annual temperature variations and an average elevation below 2000 m, this region is likely to become unsuitable for *L. meyenii* growth.

Although southern Africa includes the South African Plateau and the Drakensberg Mountains, its average elevation remains below 2000 m, and it is characterized by a tropical savanna climate, and this makes it a unsuitable habitat for *L. meyenii*. In contrast, the Tibetan Plateau, with an average elevation exceeding 4000 m, is expected to experience overall warming in the future. This warming trend is particularly pronounced in the northern region, with significant increases in winter temperatures anticipated, and this leads to a further reduction in annual temperature variation [72].

Yunnan Province in China has a subtropical monsoon climate, marked by large diurnal temperature variations, minimal annual temperature fluctuations, and mild weather throughout the year [73], and this makes it highly suitable for *L. meyenii* growth. However, under the SSP585 scenario in 2090, a contraction of suitable habitat in northwestern Yunnan was observed. likely attributed to future climate warming and decreased precipitation in the area [74].

Given the topography and projected future climatic conditions of both the southern margin of the Tibetan Plateau and Yunnan Province, we propose that the southern Tibetan Plateau may become a more favorable habitat for *L. meyenii* in the future. Additionally, the distribution of certain plant species and the area of alpine humid forests in the southern margin of the Tibetan Plateau were predicted to increase under future climate conditions [75]. We therefore suggest that this region could become one of the most suitable habitats for *L. meyenii* and recommend establishing conservation areas to support its future sustainability.

As the climate warms, shifts in plant niches may alter interspecific competition. In planning these conservation areas, it is essential to consider the interactions between herbaceous plants like *L. meyenii* and woody plants such as those found in alpine humid forests. Understanding their competitive dynamics will be crucial for ensuring harmonious coexistence among plant species, ultimately promoting the stability and development of the ecosystem.

## 5. Conclusions

Using the species distribution data of *L. meyenii* alongside multiple environmental variables, we evaluated 11 species distribution models and ultimately selected the Random Forest model as the optimal approach. This model allowed us to pinpoint the key environmental factors that influence the distribution of *L. meyenii* and to simulate its potential suitable habitats through time. We find that the distribution of *L. meyenii* is primarily influenced by elevation and temperature, while precipitation has a relatively minor impact. Specifically, *L. meyenii* favors high elevations, a low temperature annual range (bio7), and a high mean diurnal range (bio2).

Driven by climate change, the total area of suitable habitat for *L. meyenii* has decreased from the past to the future, while the area classified as highly suitable has expanded. Historically, highly suitable habitats for *L. meyenii* were mainly concentrated in western South America, with moderate suitability observed in the Tibetan Plateau. During the LGM—the MH, climate-driven changes led to the expansion of suitable habitats along the margins of the Tibetan Plateau and in Southeast Asia, while significant contractions occurred in southern and eastern Africa. However, from the MH to the present, this distribution pattern has reversed, with a contraction in suitable habitats on the Tibetan Plateau. In the future, western South America is projected to continue serving as a stable and highly suitable region for *L. meyenii*. Meanwhile, as time progresses and greenhouse gas emissions intensify, highly suitable areas along the southern margin of the Tibetan Plateau are expected to expand further. This suggests that the region may emerge as an important potential area for the cultivation and conservation of *L. meyenii*, alongside the Andes

Mountains. Centroid analysis indicates that in South America, the centroid of suitable habitats for *L. meyenii* will continue to shift northward. In East Asia, the centroid of suitable habitats shows a southeastward movement followed by a westward shift in the past, while future migration trends appear to be less pronounced.

This study will provide an important basis for better understanding the adaptation mechanisms of alpine herbaceous plants like *L. meyenii* to environmental changes and offer significant guidance for the future establishment of conservation areas for *L. meyenii*.

## Declarations

### Author contributions

Zeyu Qin: Conceptualization, Methodology, Investigation, Data curation, Writing - Original Draft, Writing - Review & Editing. Huasheng Huang: Conceptualization, Methodology, Investigation, Writing - Review & Editing, Supervision, Funding acquisition. Xuanqi Liu: Validation, Visualization, Writing - Review & Editing. Xia Meng: Validation, Visualization, Writing - Review & Editing. Mingqiao Li: Visualization, Writing - Review & Editing.

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### Data availability

Data is provided within the manuscript or supplementary information files.

### Clinical trial number

Not applicable.

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Acknowledgements

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## Competing Interest

The authors declare no competing interests.

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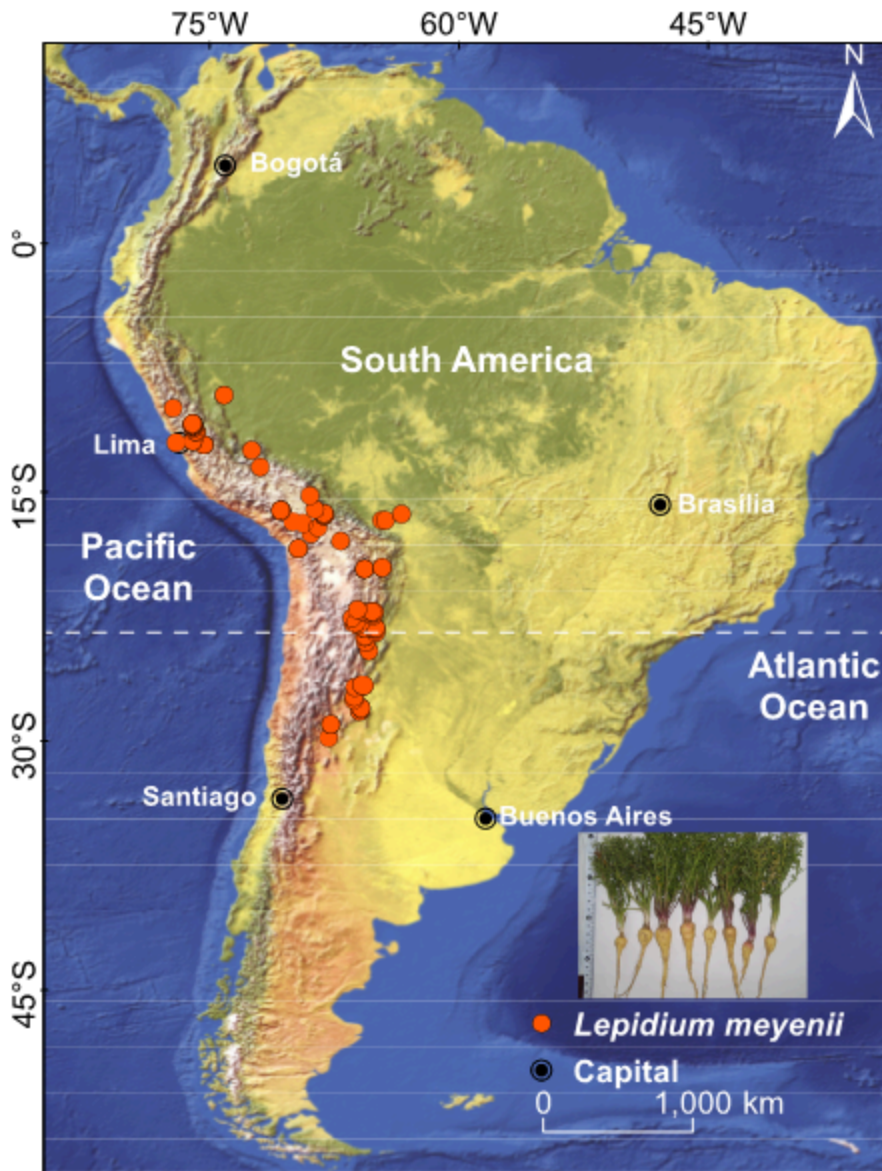
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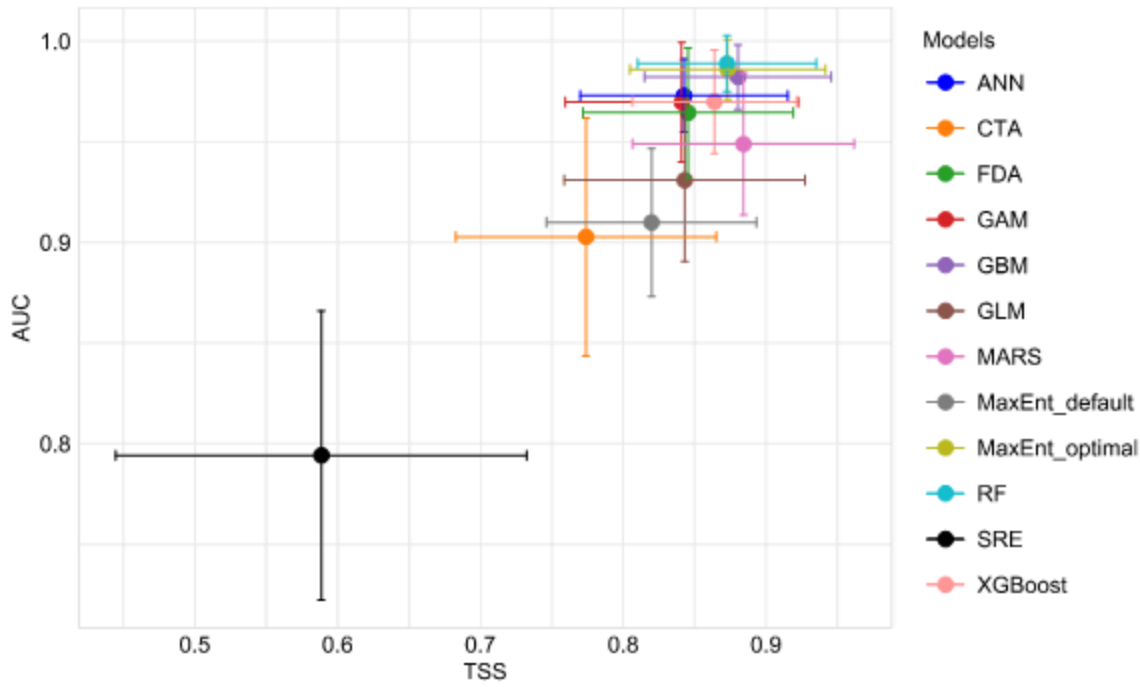
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## Figures



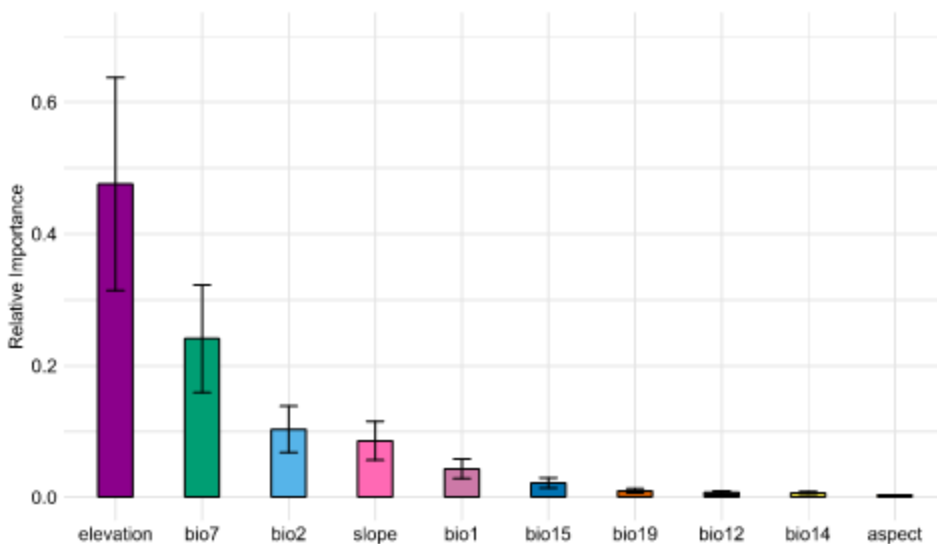
**Figure 1**

Geographically valid occurrence records of *Lepidium meyenii* sourced from GBIF (<http://www.gbif.org>). The base map and the embedded image of *L. meyenii* were obtained from Natural Earth (<https://www.naturalearthdata.com/>) and Wikipedia (<https://en.wikipedia.org/>, credit: Vahe Martirosyan, under the CC BY 2.0 license, <https://creativecommons.org/licenses/by/2.0/>), respectively.



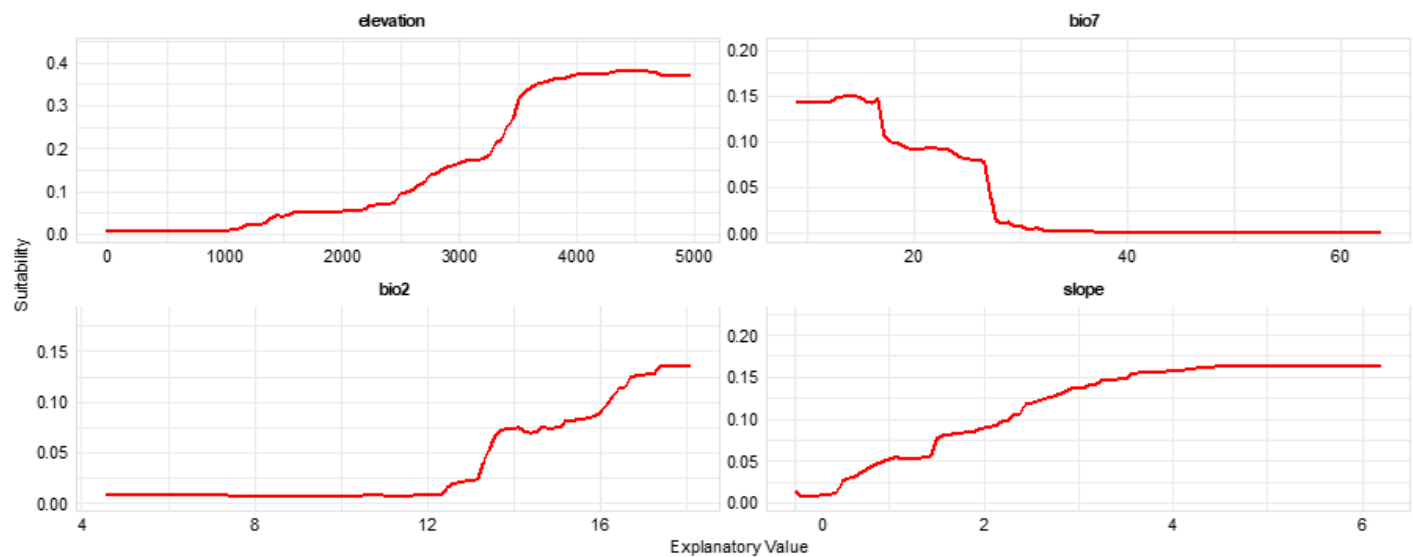
**Figure 2**

Evaluation of the accuracy of 11 models for simulating the global potential distribution for *Lepidium meyenii* using the biomod2 package. The error bars represent the standard deviation of area under the curve (AUC) and true skill statistic (TSS). The models evaluated include artificial neural network (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multiple adaptive regression splines (MARS), default parameters of the maximum entropy model (MaxEnt\_default), optimal parameters of the maximum entropy model (MaxEnt\_optimal), random forest (RF), surface range envelope (SRE), and extreme gradient boosting (XGBoost).



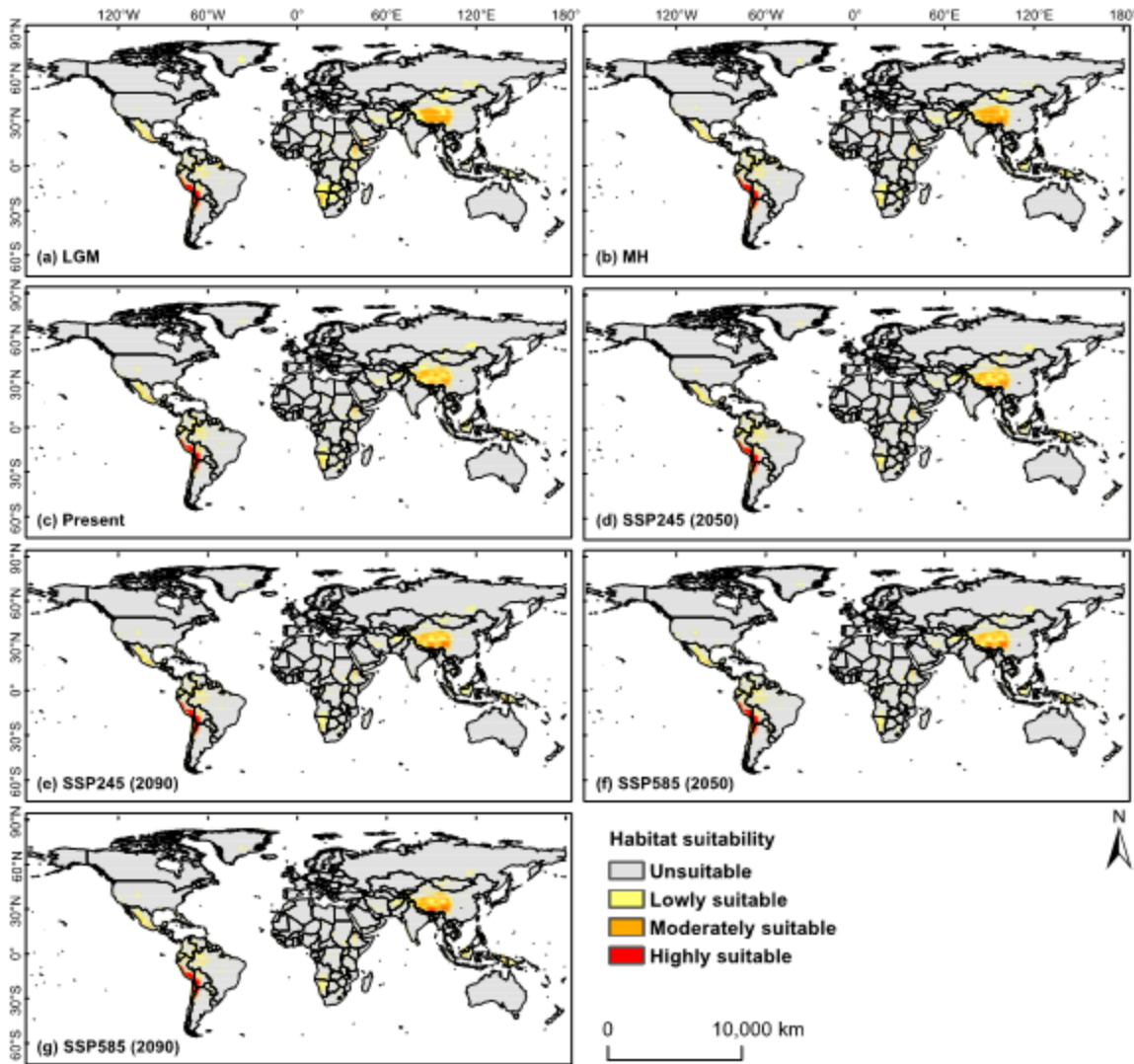
**Figure 3**

Relative importance of environmental variables on the current potential distribution of *Lepidium meyenii*. The error bars represent the standard deviation of relative importance for each environmental variable. These variables include annual mean temperature (bio1), mean diurnal range (bio2), temperature annual range (bio7), annual precipitation (bio12), precipitation of driest month (bio14), precipitation seasonality (bio15), precipitation of coldest quarter (bio19), aspect, slope, and elevation.



**Figure 4**

Response curves of the distribution of *Lepidium meyenii* in relation to the four most important environmental variables. They are elevation (meters), mean diurnal range (bio2) (°C), temperature annual range (bio7) (°C) and slope (°). The grey background indicates the fluctuations observed across multiple random simulations.



**Figure 5**

Global potential suitable distribution of *Lepidium meyenii* across different time periods using the random forest (RF) model. Abbreviations: LGM = Last Glacial Maximum, MH = Mid-Holocene. Habitat suitability classifications are as follows: unsuitable =  $0 < \text{habitat suitability value} < 0.2$ , lowly suitable =  $0.2 < \text{habitat suitability value} < 0.4$ , moderately suitable =  $0.4 < \text{habitat suitability value} < 0.6$ , highly suitable =  $0.6 < \text{habitat suitability value} < 1$ .

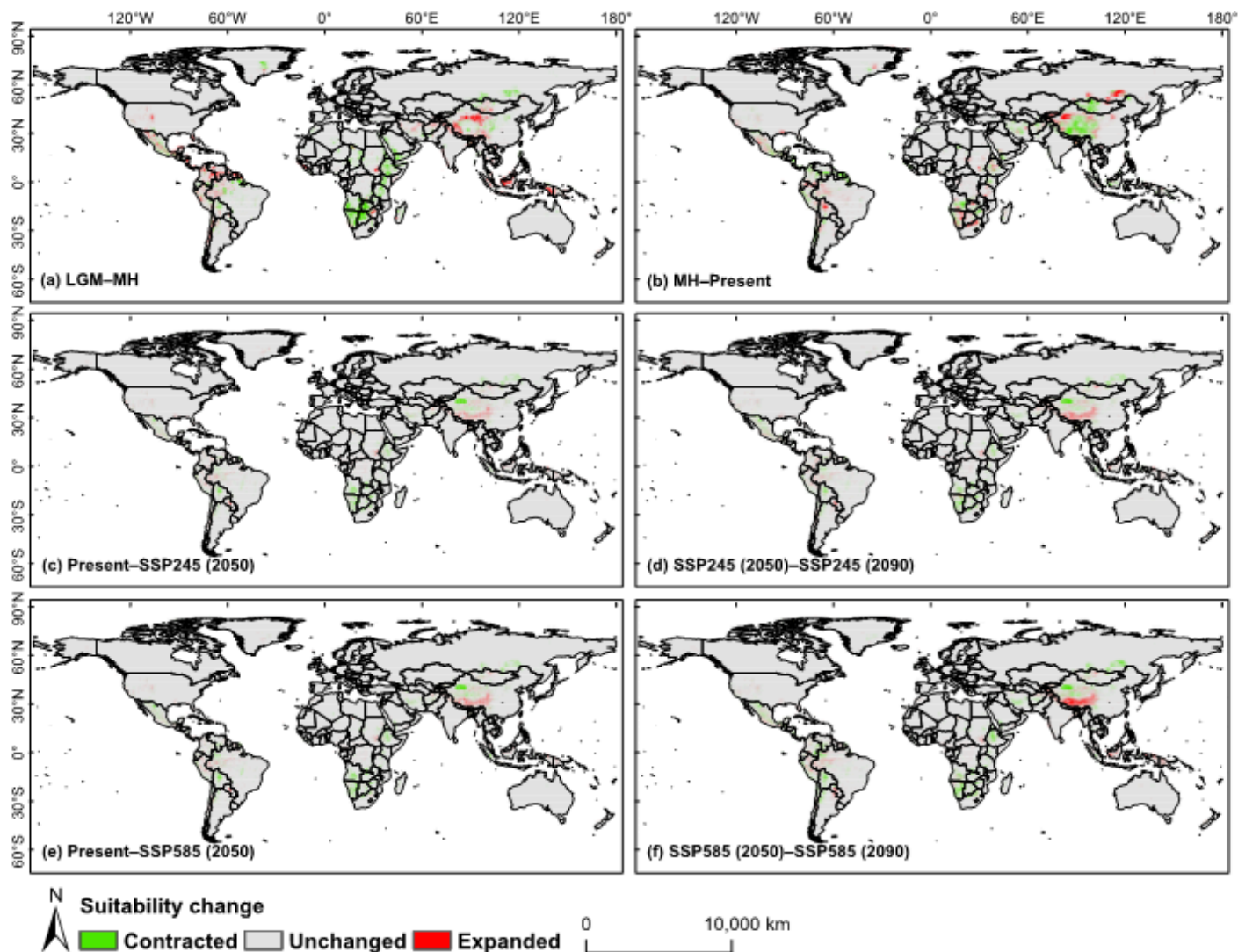
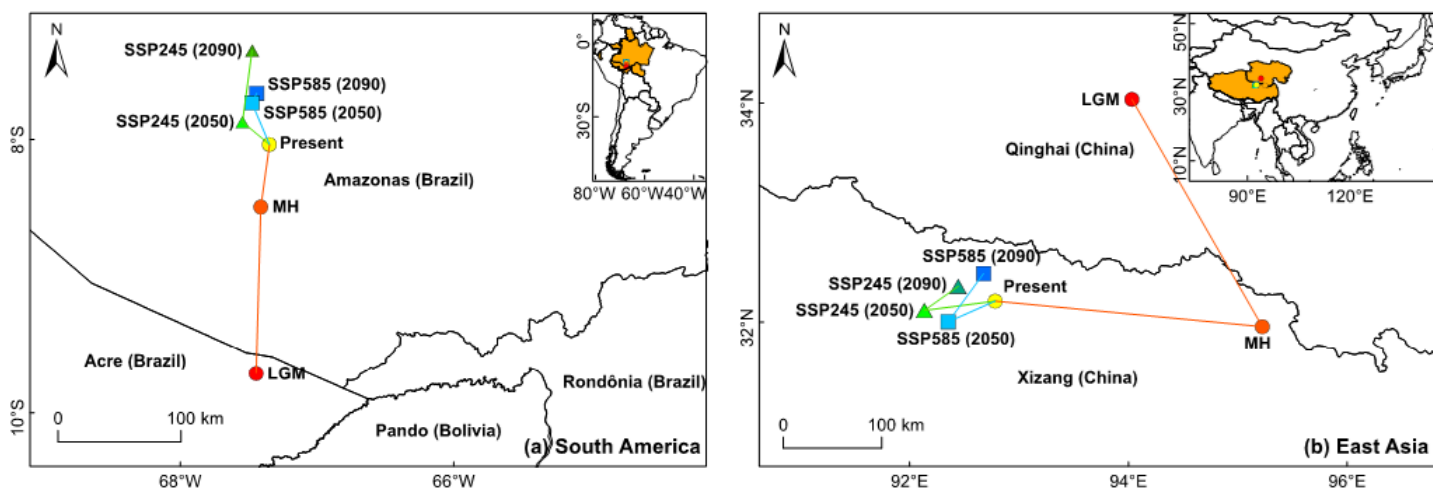


Figure 6

Temporal changes in potential suitable areas for *Lepidium meyenii* under various climate scenarios. Abbreviations: LGM = Last Glacial Maximum, MH = Mid-Holocene.



## Figure 7

Temporal changes in the migration trends of the geometric centers of potential suitable areas for *Lepidium meyenii* under various climate scenarios in South America (a) and East Asia (b). Abbreviations; LGM = Last Glacial Maximum, MH = Mid-Holocene. The lines represent the migration pathways of the centroids, and indicate centroid movement over time: orange—from the past to the present; green—from the present to the future under the SSP245 scenario; blue—from the present to the future under the SSP585 scenario.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterialQinetal.docx](#)