scientific reports

OPEN

Predicting the potential distribution of *Podophyllum hexandrum* Royle in the Himalaya under CMIP6 climate projections

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***Podophyllum hexandrum* is a globally endangered medicinal plant facing severe survival challenges. In the present study, habitat suitability modelling of *P. hexandrum* was carried out to identify potentially suitable habitats in the western Himalayas under current and future climatic scenarios using MaxEnt software. Future distribution modelling was carried out using Shared Socioeconomic Pathways; SSP126, SSP370 and SSP585 for the time period 2041–2070. MaxEnt output maps were categorized into four potential habitat suitability classes using threshold < 0.25 as "not suitable" 0.25–0.50 as "least suitable", 0.51–0.75 as "moderately suitable", and > 0.75 as "highly suitable". Furthermore, overlay analysis was used to calculate loss, gain, and no change areas. Centroid migration direction and distance were also calculated. The model revealed that the precipitation amount of the driest month and mean annual air temperature determine the distribution of *P. hexandrum*. Under future climatic scenarios, the species is predicted to undergo significant changes in its distribution losing 8.12% and 8.25% of its suitable habitats under SSP370 and SSP585 pathways, respectively. Under SSP126 pathway, the species is predicted to gain an area of 1.63%. The species is predicted to shift southeastwards under all climatic scenarios and the distance of centroid migration will increase with an increased climate extremities. Though overlapping of its suitable habitats with Protected Areas plays an important role in conserving its wild populations. The decline in number of individuals due to habitat fragmentation, low rate of natural regeneration or seed germination and prolonged dormancy is still a serious concern. There is an urgent need to frame pertinent conservation and management policies for habitat restoration and reintroduction of this species, therefore, the present study will serve as a baseline in this direction.**

Keywords Medicinal and aromatic plants, Himalayan region, Climate change, Range change, Conservation and management

Climate change is considered one of the major challenges for ecologists with its profound impacts on biodiversity, ecosystem services and sustainable development[1,2]. The impact of climate change on ecosystems has been exacerbated by the increased frequency of extreme climate events brought on by rapid urbanization and increased greenhouse gas emissions[3]. Climate is among the key factors influencing the growth and geographical distribution of species[4] and changing climatic scenarios have been identified as a potent threat to biodiversity globally[5]. However, endemic and threatened species are particularly vulnerable to climate change due to their small population sizes, narrow distribution ranges, and limited genetic diversity[6]. For their effective conservation, introduction, cultivation and sustainable utilization, it is essential to understand how these species respond to changing climatic scenarios[7,8]. Predicting the species' habitat suitability under various climatic scenarios has become a research priority, guiding the scientific community and policymakers in developing conservation and management strategies. Species distribution models (SDMs) have proven to be vital tools for ecologists in forecasting the geographical ranges of species and analyzing how the environmental variables influence their distributions[9,10].The primary inputs used by SDMs to assess climate change and its effects under various

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greenhouse gas emission scenarios at both global and regional scales are general circulation models (GCMs), developed by multiple research groups with support from the Coupled Model Intercomparison Project (CMIP)[11]. Since the 1990s, CMIP has served as a standardized conceptual framework that has significantly advanced climate science by facilitating the analysis of GCM outputs produced by research institutions worldwide[12]. The more recent CMIP6 models provide improved temperature simulations, particularly in representing atmosphere–biosphere interactions, complex topography, and with advanced model resolution compared to previous models (i.e., CMIP5). They also offer a more accurate representation of greenhouse gas concentrations, incorporating more complex biogeochemical cycles and physical processes[13,14]. CMIP6 uses diverse matrix combinations of scenarios for greenhouse gas emissions and socioeconomic development known as shared socioeconomic pathways (SSPs) that are suggested for climate projection over representative concentration pathway (RCP) scenarios used for CMIP5 future forecasts[15].

The Himalayan region, recognized as a biodiversity hotspot, harbours rich floristic and faunal diversity and possesses the highest concentration of medicinal and aromatic plants (MAPs)[16]. MAPs play a vital role in the regions's ecology, livelihoods, and cultural traditions, providing significant economic benefits to indigenous communities [17]. However, the Himalayas are highly sensitive and particularly vulnerable to the impacts of climate change[18], which is increasingly altering the habitat, distribution, ecology, and phenology of MAPs, especially at higher altitudes[19]. Coupled with climate change, MAPs face serious survival threats in the wild due to anthropogenic disturbances, habitat fragmentation and overexploitation[16]. To address these drivers of biodiversity loss, the identification of suitable habitats for the commercial cultivation of MAPs is imperative[17]. Therefore, the first step in putting conservation and management plans into action is forecasting the current and future suitable habitat for threatened MAPs. In this regard, the present study aims to predict the potential distribution of *Podophyllum hexandrum*, an endangered medicinal plant of the Himalayan region, under current and future climatic scenarios. The study was conducted to fulfill the following objectives; (a) to predict the suitable habitats of *P. hexandrum* under current climatic conditions, (b) to predict the suitable habitats of *P. hexandrum* under optimistic, moderate and pessimistic climate scenarios for the time period 2041–2070, (c) to identify the most important variables determining the distribution of *P. hexandrum*, (d) to assess the range change dynamics of *P. hexandrum* under future climatic conditions concerning current climatic conditions, e) to analyze the direction and distance of centroid migration under future climatic conditions relative to the current climate. This analysis will be useful for identifying suitable areas for species reintroduction and inform the development of effective conservation policies.

Materials and methods

Study area

The Indian Himalayan Region (IHR), with three biogeographic zones and eight provinces, extends from Arunachal Pradesh to Jammu and Kashmir[20,21]. The region is a major repository of biodiversity due to its broad elevation range and varied topography[22–24]. With 30% endemic, IHR harbours approximately half of the flowering plant species of India[25]. The region is considered critical for India's ecological security, providing vital ecosystem services and benefits to millions of indigenous people[26]. The western Himalaya, comprising Jammu and Kashmir including Ladakh (latitude 32.28–37.06 longitude 72.53–80.32), Himachal Pradesh (latitude 30.38–33.12 longitude 75.58–79.01) and Uttarakhand (latitude 28.43–31.28 longitude 77.57–81.02) (Fig. 1), holds a unique position in terms of biodiversity and cultural diversity. The region represents a geologically dynamic and ecologically diverse region shaped by active tectonics, varied climatic regimes, and complex geomorphic processes[27].Geomorphologically, the region lies within the seismically active collision zone of the Indian and Eurasian tectonic plates, characterized by ongoing uplift, frequent earthquakes, and mass wasting events[28].The climate of this region is often referred as extra-tropical mountain type and can be divided into subtropical, temperate and alpine climate types[29]. There is a great variation in the annual and diurnal temperature in this region due to continental effects. The region receives a considerable proportion of the precipitation during winter season from the Western Disturbances and the presence of extensive glaciers and snowfields strongly governs the hydrology and climate of the region[30]. It has a representative, natural, and socio-economically important biodiversity with diverse habitats, species, populations, communities and ecosystems. Also, the region is also home to various tribal groups, including Gujjar, Bakarwal, Balti, Bota, Dard, Bhoxa, Shin, Gaddi, Sippi, Bhotias, and Jaunsari[25,31,32]. Further, most of these tribal groups are mountain dwellers dependent on bioresources for their daily needs.

Targeted plant species

Podophyllum hexandrum Royle (Family: Berberidaceae), commonly known as Himalayan May Apple, is a shade-loving, erect, glabrous, succulent, high altitudinal herbaceous plant species of the Himalayan region[33]. It is distributed across the Indian Himalayan region, Bhutan, Pakistan, Afghanistan, Nepal, Taiwan, and China (POWO; https://powo.science.kew.org). The species thrives best on alpine slopes, forest openings/margins, and damp, shaded sub-alpine forest floors[34]. Mature individuals of *P. hexandrum* grow to a height of 15–60 cm tall and possess creeping rootstock. The leaves are alternate with long petioles and broad lamina, palmately divided into 3 broadly elliptic segments[31]. The flowers are large, 3.8–5 cm in diameter, white, bisexual, with 6 stamens and numerous ovules. The fruit is a berry, elliptic or ovoid in shape, turning orange or red at maturity containing numerous seeds (Fig. 2). In traditional healthcare systems (Ayurveda, Unani, Siddha, Tibetan and Chinese medicine), *P. hexandrum* is used to treat a variety of diseases and ailments such as constipation, fever, jaundice, liver disorders, syphilis, and lymph gland-related diseases[35]. The rhizomes of *P. hexandrum* contain a high concentration of Podophyllotoxin, a compound used in the production of semi-synthetic anticancer drugs such as etoposide, teniposide, and etoposide phosphate[36]. As a result, the plant is being uprooted in large quantities through unscientific practices, leading to a significant decline in its wild populations. Moreover, it is a

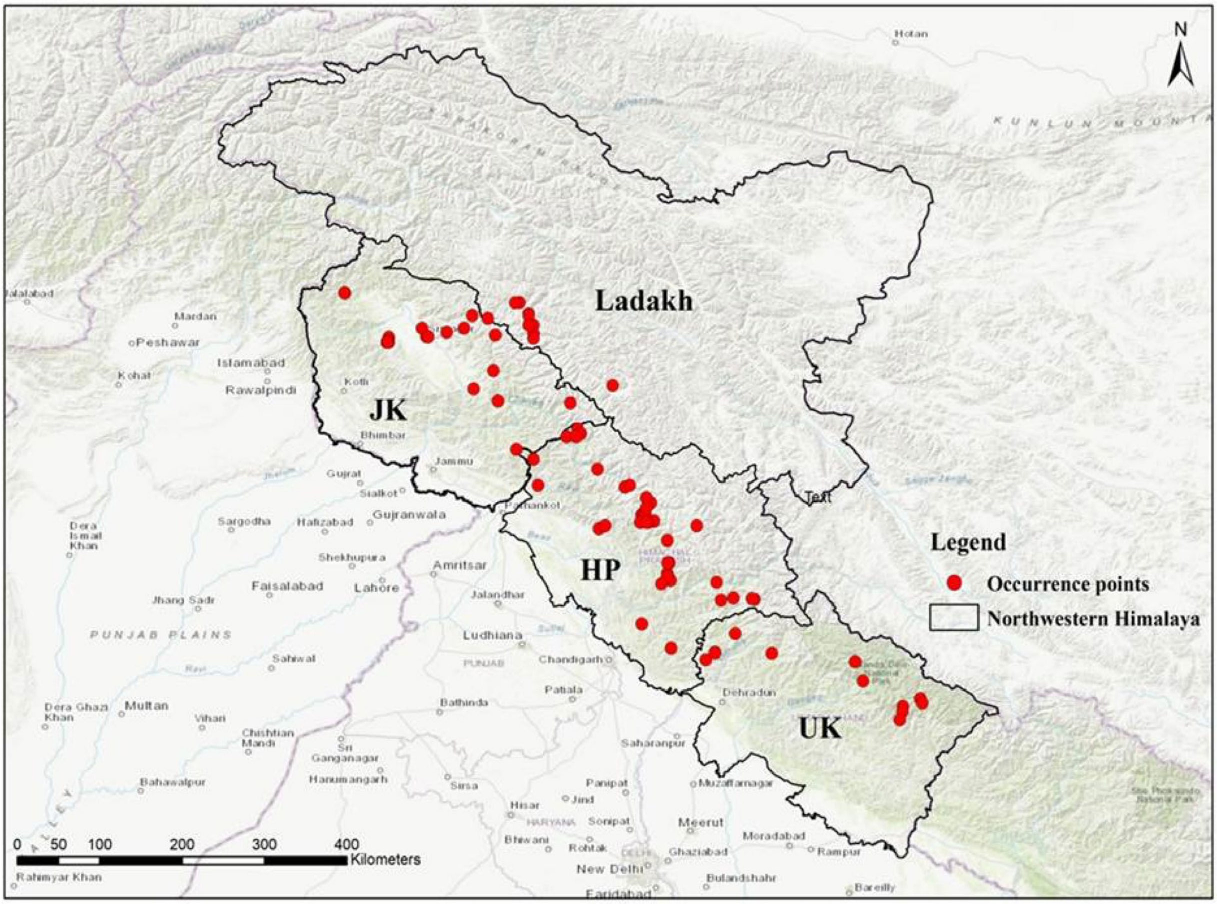

Fig. 1. Map showing the location of study area along with occurrence points of *Podophyllum hexandrum*.

slow-growing species that primarily propagates through seeds, which exhibits a low seedling survival rate[37]. Due to overexploitation and poor natural regeneration, the species has been categorized as globally endangered[38] and requires immediate conservation action.

Species distribution modelling

Occurrence data

Distribution records of *P. hexandrum* were collected from both primary and secondary sources. Field surveys were conducted between 2018 and 2023, involving the establishment of systematic transects within the area of interest across different ecological habitats. Coordinates of each location where *P. hexandrum* was encountered were recorded using high-precision Garmin Global Positioning System (GPS). Plant specimens were collected from Gulmarg Wildlife Sanctuary, Kashmir Himalaya and field photographs were also taken for precise morphological identification. The collected plant specimens were identified using local floras, and their correct identification was further confirmed at the Centre for Biodiversity Studies, Baba Ghulam Shah Badshah University, Rajouri, Jammu and Kashmir. Herbarium specimens of correctly identified plant were deposited in the Herbarium of the Centre for Biodiversity Studies, Baba Ghulam Shah Badshah University, under voucher number BGSBU/048. Furthermore, an extensive literature review was conducted to collect occurrence points from published sources, including research papers, theses and online databases such as the Global Biodiversity Information Facility (GBIF). A total of 132 occurrence points were collected from primary and secondary sources that were screened for accuracy, and processed to reduce sampling bias and inaccuracy, as occurrence points carry an inherent risk of bias and errors[39]. To achieve this, occurrence records with no spatial coordinates or specific locations, those showing obvious identification errors, and those with unreliable distribution were removed. Furthermore, duplicates and records older than 50 years were also excluded. Occurrence points are often skewed towards easily accessible geographic areas, leading to spatial autocorrelation and potential over-fitting[40]. To mitigate these effects, sampling bias correction was performed as an important step to minimize the potentially strong influence of spatial autocorrelation on the modelling predictive ability and subsequent interpretation[41]. For this, all occurrence records were subjected to spatial rarefaction, which summarized numerous occurrence points into a single point within the specified distance (1 × 1 km grid), and spatially autocorrelated occurrence locations were removed using the SDM toolbox in ArcGIS 10.8. This resulted in a final dataset comprising 83 unique occurrence points, which were saved in CSV format before being used as input in MaxEnt software. ArcGIS

Fig. 2. Field photographs showing the morphological characteristics of *Podophyllum hexandrum* (**A**) Vegetative stage; (**B**) Flowering stage; (**C**) Fruiting stage.

10.8 was used to create a distribution map based on these data points, providing valuable insights for subsequent research endeavours and confirming the accuracy and reliability of the distribution dataset.

Environmental data

We downloaded nineteen current (1981–2010) bioclimatic variables at a 30 arc second spatial resolution from the Climatologies at High Resolution for the Earth Land Surface Areas (CHELSA) database version 2.1 (https://chelsa-climate.org/). Future climatic data for the time period 2041–2070 were downloaded from Coupled Model Intercomparison Project 6 (CMIP6) for three Shared Socioeconomic Pathway (SSP) climatic scenarios: SSP126 (optimistic), SSP370 (moderate) and SSP585 (pessimistic). The obtained raster data were then processed using ArcMap 10.8, which included resampling, cropping, and masking in accordance with the study area's boundary using the same coordinate system (WGS 1984). The modeling process in MaxEnt may become complicated by highly correlated variables, which could impact the model's overall ability to predict species distribution[42]. Recent findings[43] suggest that lowering the number of covariates is therefore thought to be crucial for improving the precision of species distribution estimation. We used a Pearson correlation test for the 19 bioclimatic variables to prevent the distortion of MaxEnt model estimation caused by multi-collinearity among the variables. For any pair of variables with a Pearson's r greater than 0.7, we selected the bioclimatic variable with a higher percent contribution. After that, we chose five bioclimatic variables to model the distribution of *P. hexandrum*. These variables included mean annual air temperature (Bio1), mean diurnal air temperature range (Bio2), annual range of air temperature (Bio7), annual precipitation amount (Bio12) and precipitation amount of the driest month (Bio14). The filtered occurrence records and five bioclimatic variables, in CSV and .ascii formats respectively, were imported into MaxEnt as sample data and environmental layers, respectively.

MaxEnt modelling

In the present study, the Maximum Entrophy (MaxEnt) version 3.4.4 (https://biodiversityinformatics.amnh.org/open_source/maxent/) algorithm was used to predict the distribution of *P. hexandrum* under current and future climatic scenarios. MaxEnt has been extensively validated for its high predictive accuracy, particularly in scenarios involving presence-only data and limited occurrence records. Its algorithmic flexibility and computational efficiency make it a preferred choice for species distribution modeling, especially for rare or data-deficient taxa[44,45]. We ran the algorithm using auto features, which allow MaxEnt to automatically select appropriate feature classes based on the number of occurrence records, thereby optimizing model performance and complexity. We used ten replicate runs with a cross-validated approach to assess model stability and accuracy. A total of 10,000 background points with maximum iterations of 2000, default prevalence of 0.5, and 10th percentile training presence threshold rule was used. Occurrence records were split into 75% for model training and 25% for testing. The relative importance of predictor variables was assessed using the jackknife method. The accuracy of the model was evaluated with the Receiver Operating Characteristic (ROC) curve, Area Under the Curve (AUC) and True Skill Statistic (TSS). AUC is considered one of the best measures for estimating the suitability of a species' environment, especially when background data are used[46]. According to a recent study[47], the AUC value of a model ranges from 0 to 1, and model performance can be assessed as excellent (>0.9), good (0.8–0.9), fair (0.7–0.8), poor (0.6–0.7), and failing (<0.6).TSS was calculated using binary predictions to create a confusion matrix consisting of true positives (observed presence correctly predicted as presence), true negatives (observed absence correctly predicted as absence), false positives (observed absence falsely predicted as presence) and false negatives (observed presence falsely predicted as absence). These confusion matrix values were used to calculate Sensitivity and Specificity as;

$$Sensitivity = \frac{True\ positives}{True\ positives + False\ negatives}$$

$$Specificity = \frac{True\ negatives}{True\ negatives + False\ positives}$$

Finally, TSS was calculated as;

$$TSS = Sensitivity + Specificity - 1$$

TSS values range between −1 to+1, and values above 0.5 indicate acceptable model performance. Once the model was standardized for the current distribution prediction, the same settings were used to predict the future distribution under each scenario. Thus, the final output of the modelling generated four maps: one for current and one for each future climatic scenario.

Classification of predicted habitats

The final output of the MaxEnt model is the potential habitat suitability distribution, expressed as a habitat suitability index ranging from 0 to 1. Values close to 1 represent highly suitable habitats, while values close to 0 indicate unsuitable areas for the species. The habitat suitability map was subsequently categorized into four potential habitat classes: values<0.25 as "not suitable", 0.25–0.50 as "least suitable", 0.51–0.75 as "moderately suitable", and>0.75 as "highly suitable". The same classification criteria were applied to both current and future prediction maps and the area under each category was calculated for all scenarios. All categorized prediction maps were converted to KML format to identify suitable habitats in Google Earth Pro.

Range change

Prediction maps for current and future scenarios were converted to binary form (presence/absence) using the threshold<0.5 (absence) and>0.5 (presence). To evaluate how the amount of suitable habitat will change in the future under various emission scenarios compared to the current, we used overlay analysis to calculate loss, gain, stable, and absent areas. Loss designates the areas that are currently suitable and are predicted to become unsuitable in future, and gain designates the currently unsuitable areas and predicted to become suitable in the future. Further, stable designates the areas that are predicted to be suitable under current as well as future scenarios, and absent designate the areas that are predicted to be unsuitable under both current and future climatic scenarios. Further, using the binary maps, altitudinal range of suitable habitats under current and each future scenario was calculated using Digital Elevation Model (DEM) downloaded from WorldClim (www.Worldclim.org).

Range change calculations:

$$Loss = Overall\ suitable\ area\ (current) - Overall\ suitable\ area\ (future\ scenario)$$

$$Gain = Overallsuitablearea\,(Futurescenario) - Overallsuitablearea\,(Current)$$

$$Net\ change = Gain - Loss$$

$$Percentage\ range\ change = \frac{Net\ change}{Overall\ suitable\ area\ (Current)} \times 100$$

Centroid migration direction and distance

The population centroid is the representative indicator reflecting the population movement process[48]. In the present study, centroid migration direction and distance were calculated using R software version 4.4.2 (https://www.R-project.org/). Binary maps in raster format were used as inputs to calculate the centroids of presence areas (threshold≥0.5) for both current and future distribution prediction maps, using the '*st_centroid*' function from the '*sf*' package. Pairwise migration distance (in kilometers) and direction between the centroids of different scenarios were calculated using the '*distGeo*' function from the '*geosphere*' package.

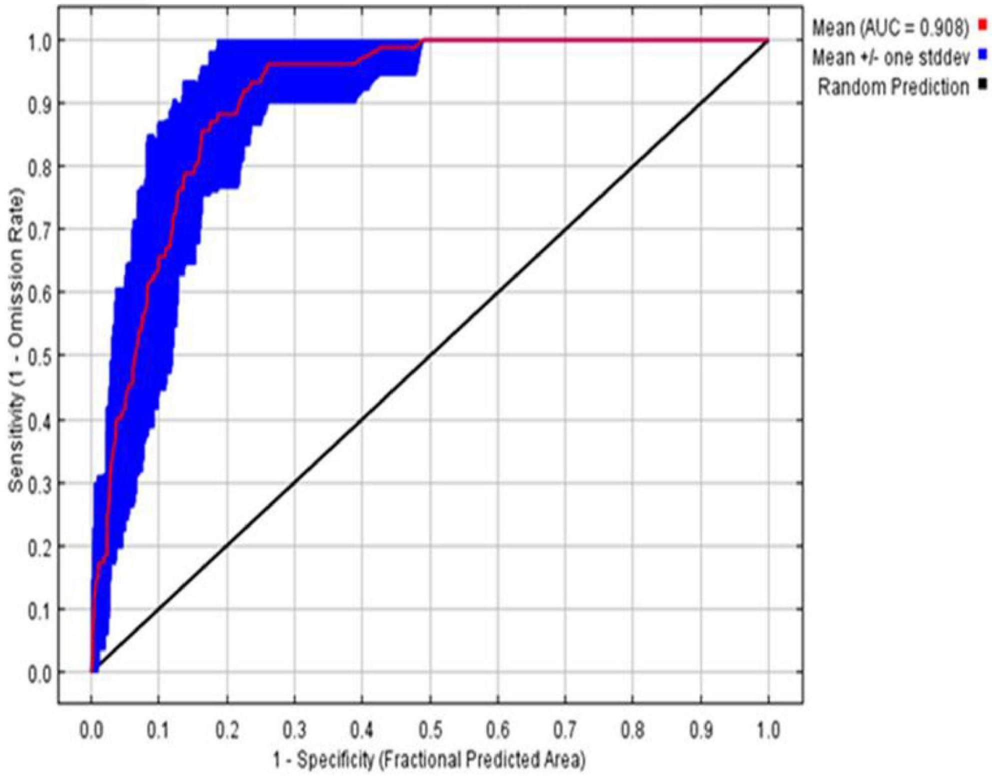

Fig. 3. Receiver Operation Characteristic (ROC) for *Podophyllum hexandrum* showing Area Under Curve.

Biovariables	Description	Unit	Explanation	Percent contribution	Permutation importance
Bio1	mean annual air temperature	°C	mean annual daily mean air temperatures averaged over 1 year	40.6	40.1
Bio2	mean diurnal air temperature range	°C	ratio of diurnal variation to annual variation in temperatures	1.6	6.6
Bio7	annual range of air temperature	°C	The difference between the Maximum Temperature of Warmest month and the Minimum Temperature of Coldest month	7	18
Bio12	annual precipitation amount	kg m^{-2} $year^{-1}$	Accumulated precipitation amount over 1 year	2.4	2.3
Bio14	precipitation amount of the driest month	kg m^{-2} $month^{-1}$	The precipitation of the driest month	48.3	33.1

Table 1. Description, percentage contribution and permutation importance of selected bioclimatic variables.

Results

Model performance and variable importance

The AUC value for current and future models was 0.90 ± 0.03, indicating excellent model performance. Figure 3 presents the relative contribution of the environmental variables in determining the distribution of *P. hexandrum*, as predicted by the model. Additionally, the models yielded a TSS value of 0.64, indicating good model performance. Based on variable importance analysis, the model identified Bio14 (precipitation amount of the driest month) and Bio1 (mean annual air temperature) as the most important variables, contributing 48.3% and 40.6%, respectively, to the predicted distribution of *P. hexandrum*. These two variables exhibited the highest permutation importance also, indicating that the predictions heavily rely on them (Table 1). Other variables, including Bio2 (mean diurnal air temperature range), Bio7 (annual range of air temperature) and Bio12 (annual precipitation amount), were predicted to have a minimal contribution and low permutation importance. The jackknife test for *P. hexandrum* further confirmed that Bio14 and Bio1 are the most significant variables, while Bio2, Bio7 and Bio12 are the least important (Fig. 4). Bio1 appears to provide the most useful information, as it yields the highest gain when used alone. It also contains unique information not present in other variables, as evidenced by the maximum decrease in gain when it is excluded from the model.

Predicted distribution of *P. hexandrum* under current climate scenarios

Under current climatic conditions, *P. hexandrum* is predicted to be distributed in parts of Jammu and Kashmir, Himachal Pradesh and Uttarakhand. Most parts of Ladakh are predicted to be either not suitable or only least suitable for the species (Fig. 5). Overall, 82.12% and 10.57% area of the study area are precited to be unsuitable

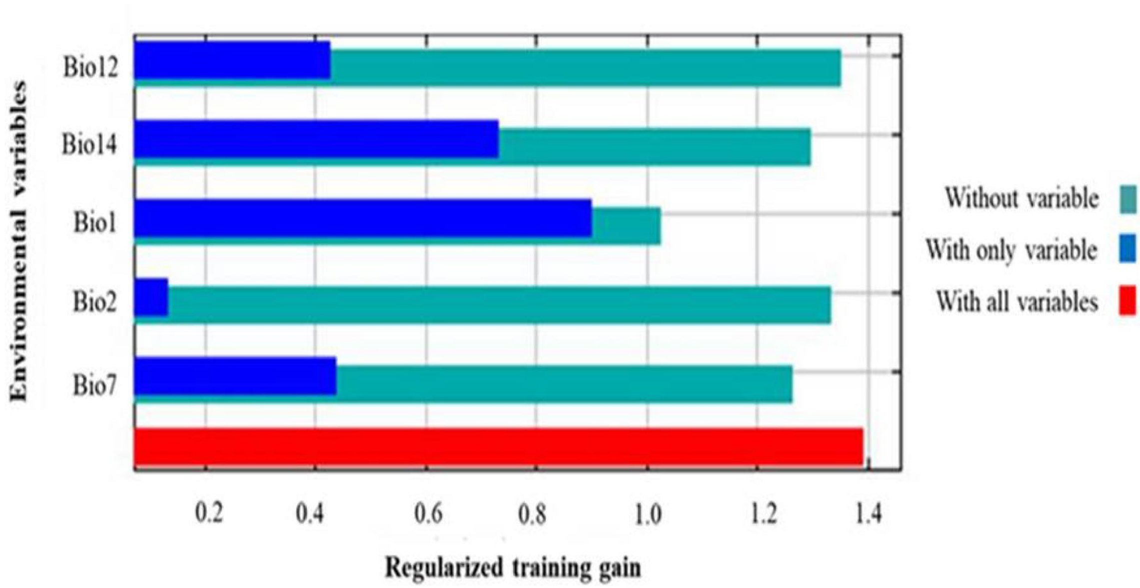

Fig. 4. Jackknife test showing the importance of selected variables in determining the distribution of *Podophyllum hexandrum*.

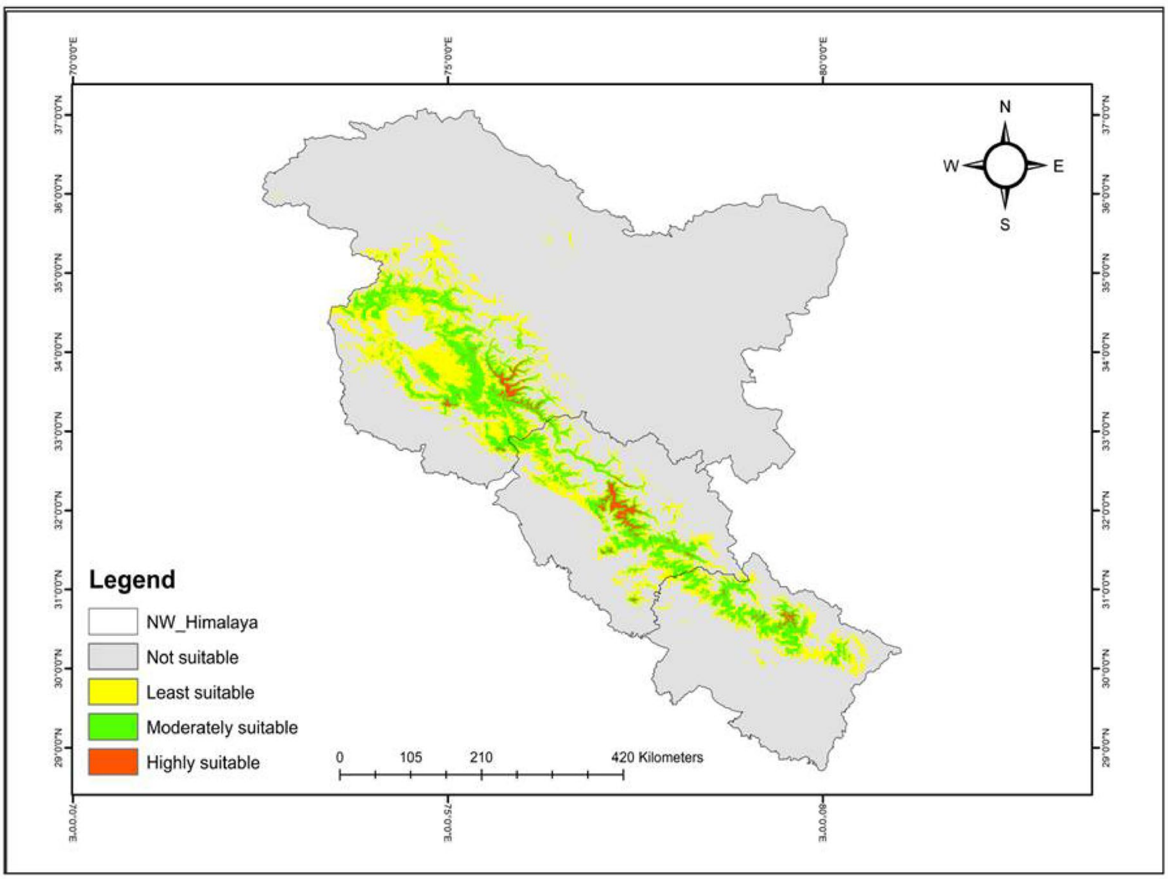

Fig. 5. Predicted distribution of *Podophyllum hexandrum* under current climatic scenarios.

Scenario	Not suitable (km^2)	%age	Least suitable (km^2)	%age	Moderately suitable (km^2)	%age	Highly suitable (km^2)	%age
Current	208,720.7	82.12	26,883.48	10.57	16,854.87	6.63	1692.51	0.66
SSP126	209,328.1	82.36	26,124.74	10.27	17,157.91	6.75	1540.82	0.60
SSP370	210,130.2	82.67	26,236.2	10.32	16,122.29	6.34	1662.86	0.65
SSP585	210,127.3	82.67	26,242.66	10.32	15,863.53	6.24	1918.1	0.75

Table 2. Potential predicted areas for *Podophyllum hexandrum* under current and future climatic scenarios.

	Current (area in %age)				SSP126 (area in %age)				SSP370 (area in %age)				SSP585 (area in %age)			
State	NS	LS	MS	HS	NS	LS	MS	HS	NS	LS	MS	HS	NS	LS	MS	HS
JKL	85.88	8.74	4.99	0.40	85.77	9.06	4.86	0.31	85.99	8.81	4.79	0.42	86.64	8.98	4.00	0.38
HP	70.64	15.88	11.52	1.96	69.74	16.33	11.94	1.99	69.59	16.67	11.85	1.90	68.46	17.03	12.27	2.25
UK	80.67	10.69	8.22	0.44	80.43	10.72	8.31	0.56	81.19	11.68	6.62	0.53	80.29	11.29	7.97	0.45

Table 3. State wise potential predicted areas for *Podophyllum hexandrum* under current and future climatic scenarios. *JKL* Jammu Kashmir and Ladakh, *HP* Himachal Pradesh, *UK* Uttarakhand, *NS* Not suitable, *LS* least suitable, *MS* moderately suitable, *HS* highly suitable.

and least suitable, respectively. Only 6.66% and 0.66% of the area are precited to be moderately and highly suitable, respectively (Table 2). Based on the state-wise analysis, it is revealed that in Jammu and Kashmir, 4.99% and 0.40% of total area are predicted to be moderately and highly suitable for the plant, respectively. In Himachal Pradesh, 11.52% and 1.96%, and in Uttarakhand, 8.22% and 0.44% of total area are predicted to be moderately and highly suitable for the plant under current climatic conditions (Table 3).Using the KML file of the prediction map, moderately and highly suitable areas were identified. In Jammu and Kashmir, Pahalgam, Padder, Gulab Garh, Qaderna, Chanjer, Anyar and Sonder are predicted to be highly suitable for the plant whereas Gulmarg, Baba Reshi, Aharbal, Hirpora, Aru, Dachigam, Trigam, Keran, Gurez, Sonamarg, Badimarg, Khodmarg, Chananwadi, Baderwah, Yousmarg, Poshiana, and Behrangala are predicted to be moderately suitable. In Himachal Pradesh, Kasol, Mashyar, Tosh, Parli, Pini, Khir Ganga, Manali, Kothi, Devidarh and Chippni are predicted to be highly suitable whereas Dehnasae, Palan, Kais, Sujanpur, Mushyar, Hadsar, Bharara,and Lahaul-Spiti are predicted to be moderately suitable for the plant. In Uttarakhand, Badrinath, Hemkund, Govind Ghat, Auli, Chanap valley trek, Bharichak-Urgam, Lambagad, Gaundhar, and Ganganani are predicted to be highly suitable whereas Rupin range, Singtur range, Supin range, Bhinlgana range, Kedarnath, Tungnath, Rudranath, Joshimath, Tapovan, Munsyari, Manal top, Pipalkoti and Dayara Bugyal are predicted to be moderately suitable for *P. hexandrum*. The highly and moderately suitable habitats of *P. hexandrum* are also predicted to overlap with protected areas, including Kishtwar National Park, Gulmarg Wildlife Sanctuary, Dachigam National Park, Hirpora Wildlife Sanctuary and Overa Aru Wildlife Sanctuary in Jammu and Kashmir; the Great Himalayan National Park in Himachal Pradesh; and Kedarnath Wildlife Sanctuary and Govind Pashu Vihar National Park and Sanctuary in Uttarakhand. The altitudinal range of the overall suitable habitats (moderately + highly suitable) of *P. hexandrum* is predicted to range from 2194 to 4263 m asl.

Predicted distribution of P. hexandrum under future climate scenarios

Under future climatic scenarios, the distribution of *P. hexandrum* is precited to undergo range change dynamics, with changes in overall suitable habitats under each climatic scenario (Fig. 6). Under SSP126, 82.36% of the total area is predicted to be not suitable, 10.27% as least suitable, 6.75% as moderately suitable and 0.60% as highly suitable for the plant. Under SSP370, 82.67% of the total area is predicted to be not suitable, 10.32% as least suitable, 6.34% as moderately suitable and 0.65% as highly suitable for the plant. Under SSP585, 82.57% of the total area is precited to be not suitable, 10.32% as least suitable, 6.34% as moderately suitable and 0.75% as highly suitable for the plant (Table 2). Although the highly suitable habitats tend to increase from current to SSP585 from 0.66% to 0.75%, the moderately suitable habitats tend to decrease from 6.63% to 6.24%. In Jammu and Kashmir, 4.86% and 0.31%, 4.79% and 0.42% and 4% and 0.38% of the total area are predicted to be suitable for the plant under SSP126, SSP370 and SSP585, respectively. In Himachal Pradesh, 11.94% and 1.99%, 11.85% and 1.9% and 12.27% and 2.25% of the total area are predicted to be suitable for the plant under SSP126, SSP370 and SSP585, respectively. In Uttarakhand, 8.31% and 0.56%, 6.62% and 0.53%, and 7.97% and 0.45% of total area are predicted to be moderately and highly suitable for the plant under SSP126, SSP370 and SSP585, respectively (Table 3). Overall, the species is predicted to lose its suitable habitats under all future climatic scenarios. Further, the altitudinal range of the suitable habitats is also predicted to deviate from the current altitudinal range. Under SSP126, SSP370 and SSP585, the altitudinal range of suitable habitats is predicted to ranges from 2206–4306, 2207–4346, and 2132–4284 m asl, respectively.

Range change dynamics

Under future climatic scenarios, the distribution of *P. hexandrum* is predicted to undergo significant changes concerning its current distribution. Under the pessimistic scenario, the range change dynamics are predicted to be more prominent. Under SSP126, the species is predicted to gain 1.63% of its suitable habitats, although it will

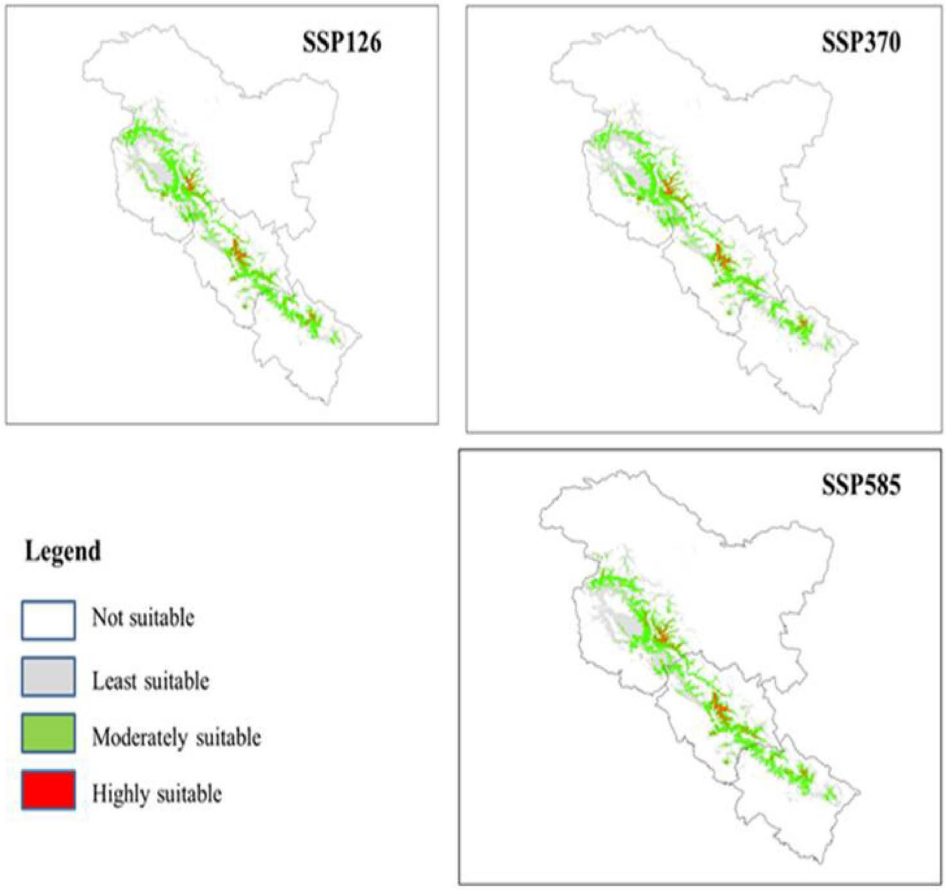

Fig. 6. Predicted distribution of *Podophyllum hexandrum* under different future climatic scenarios.

lose some of its highly suitable areas, especially in Jammu and Kashmir. Under SSP370, the species is predicted to lose 8.12% of its suitable habitats, more specifically in Jammu and Kashmir and Uttarakhand. Under SSP585, the species is predicted to lose 8.25% of its suitable habitats, specifically in Jammu and Kashmir, and Uttarakhand. Under all future climatic scenarios, Jammu and Kashmir is predicted to be more prone to losing most of its suitable habitats. In contrast, Himachal Pradesh is predicted to gain suitable areas for *P. hexandrum* (Fig. 7). Kashmir Valley is predicted to lose most of its suitable habitats, particularly from Gulmarg, Khag, Pakherpora, Baba Reshi, Aharbal, Hirpora, Sonamarg, Pahalgam, and Chandanwari. Furthermore, areas such as the Loran, Gulab Garh and Sander areas in Jammu division are also predicted to become unsuitable for *P. hexandrum* in the future. However, some areas, including Yousmarg, Kandiwara, Shangus, Brah, Wantraag, Mattan and Drass are predicted to become suitable for the plant in the future. The distribution of *P. hexandrum* is predicted to be less affected by the climate change scenarios in Himachal Pradesh, with most of the currently suitable habitats expected to remain stable. Additionally, many areas such as Kullu, Tindi, Shakoli, Kugti and Burwa are predicted to become suitable for the plant in the future. In Uttarakhand, however, the distribution of *P. hexandrum* is predicted to be severely affected, with loss of its suitable habitats in areas like Rilkot, Dwali, Jhuni, Dangugwar, Pipalkot, Gaundhar, Sari, Joshimath and Sutol. On the other hand, some currently unsuitable areas, such as Tausi, Sonprayag, and Osala, are predicted to become suitable for the plant in the future.

Centeriod migration and direction
Under all future climatic conditions, *P. hexandrum* is predicted to undergo significant range shifts. The species is expected to migrate towards the southeast under all climatic scenarios, as indicated by the centroid positions shown in Fig. 8A.The centroid deviates from its current location in all future scenarios, with the most pronounced shift observed under SSP585. The distance of centroid migration ranges from 1.88 km (Current to SSP370) to 24.5 km (Current to SSP585), as shown in Fig. 8B.

Discussion
Developing strategies to address potential changes in the habitat, distribution, ecology, and phenology of the Himalayan MAPs has become increasingly complex due to global climate change[17]. One of the most critical conservation approaches for MAPs is identifying suitable habitats for species reintroduction and cultivation, particularly to mitigate the impact of overharvesting driven by high commercial demand. Species Distribution Modelling (SDM) serves as practical ecological tool for understanding and predicting the spatial distribution

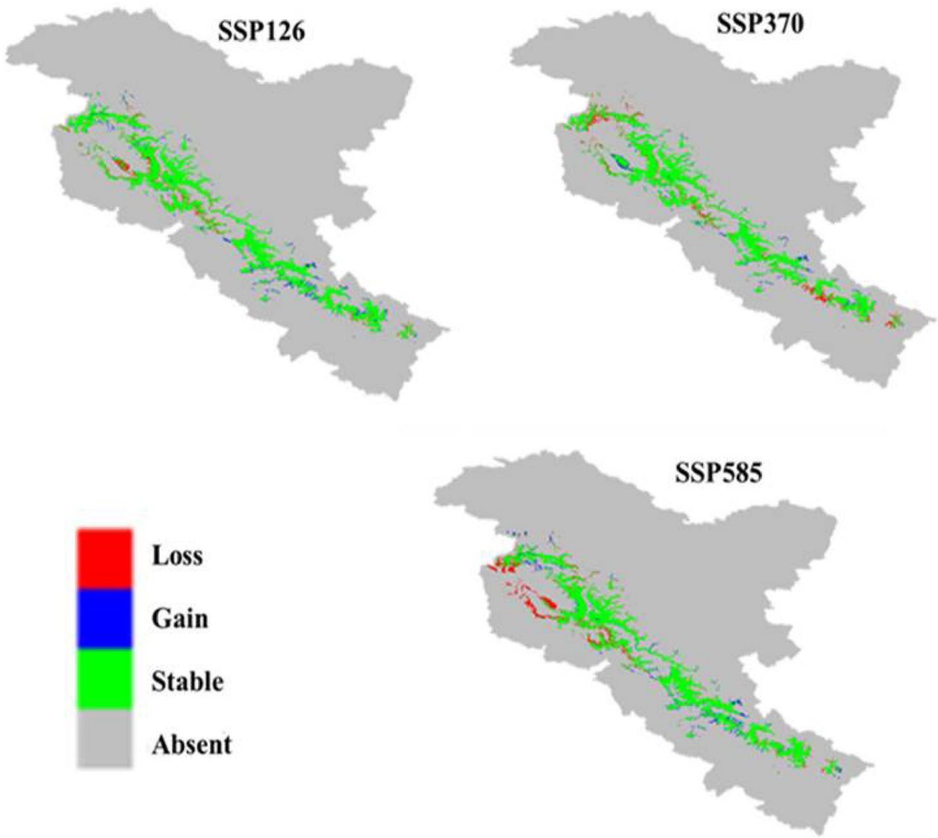

Fig. 7. Range change dynamics (loss, gain, stable and absent) of the distribution of *Podophyllum hexandrum* under future climatic scenarios with respect to the current climatic conditions.

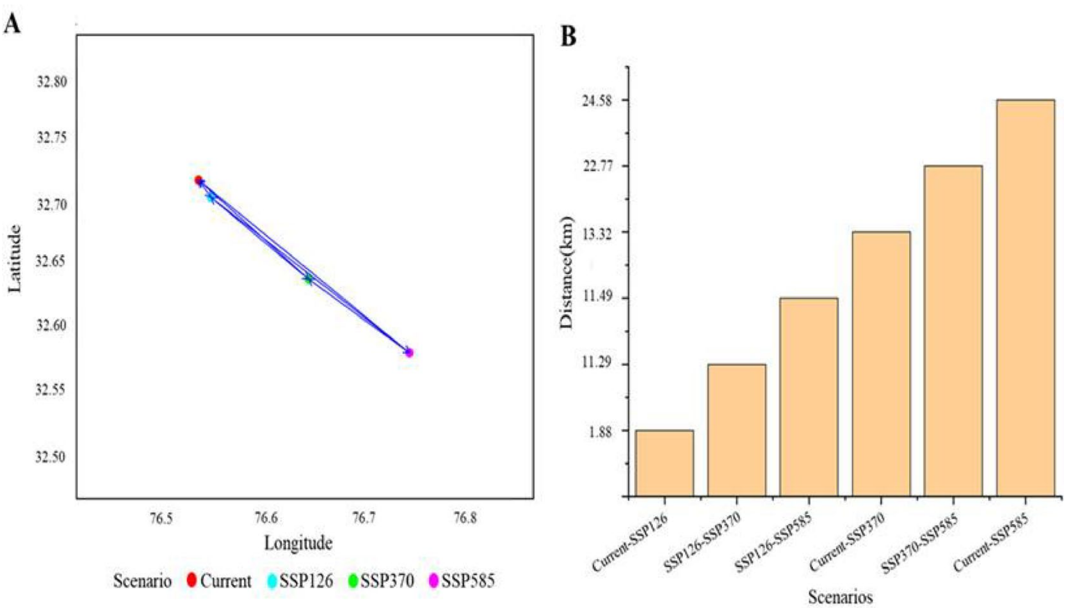

Fig. 8. Predicted centroid distributional shifts of *Podophyllum hexandrum* under different climatic scenarios (**A**) Centeriod migration direction (**B**) Centroid migration distance.

of species. They are particularly valuable for generating informative maps of potential species distribution, thereby aiding in the development of effective conservation strategies for threatened taxa[26]. Although SDM have certain limitations, its predictions continue to provide valuable insights for future assessments of suitable adaptation strategies at both ecosystem and community levels, helping to mitigate the impacts of climate change on biodiversity[32]. The present study offers robust statistical validation and potential distribution maps of *P. hexandrum*, utilizing available occurrence records and environmental data. Model performance and predictive accuracy were assessed by AUC, and TSS, both of which are widely recognized as strong indicators of model reliability and predictive power[49]. Our model achieved an AUC value of 0.90 and TSS value of 0.64, indicating high performance. Typically, models with AUC > 0.85 and TSS > 0.6 are considered reliable and demonstrate excellent performance[3,50]. Moreover, the low variability across replicates reflects stable and consistent. Therefore, our model demonstrates excellent accuracy, consistency, and robustness in predicting suitable habitats for *P. hexandrum*.

The ecology and population sizes of species can be impacted significantly by changes in patterns of temperature and precipitation, which may also alter their distribution ranges[16,51]. In the present study, analysis of the environmental factors in the model revealed that precipitation- and temperature-related variables greatly influenced the distribution of *P. hexandrum*. Both excessively high and excessively low levels of precipitation and temperature result in a near-zero probability of occurrence of *P. hexandrum*. While sufficient water availability boosts photosynthetic efficiency, improves root and leaf development, and ultimately increases biomass, water stress presents serious tribulations for plant health by inducing the expression of stress-responsive genes[52]. A study[53] has revealed that *P. hexandrum* plants exhibited a reduction in transpiration rate by 38.9%, consequently repressing the photosynthesis rate by 66.7% upon water deprivation for 15 days; thus, *P. hexandrum* is considered intolerant to dry conditions[54]. On the other hand, in the native range of *P. hexandrum*, drought-like conditions are expected to be induced by fluctuating water availability and increased water deficit[53], questioning its survival in future.

The findings of the present study indicate that the suitable habitats of *P. hexandrum* are expected to decline under projected climate change. The species is predicted to lose 8.25% and 8.21% of its suitable habitats from the northwestern Himalayas under SSP370 and SSP585, respectively. Shrestha et al.[16] have also predicted a loss of 74% of its suitable habitats by 2050 in Nepal. The impact of changing climatic scenarios varies from the northwestern to western Himalaya. The habitat suitability of *P. hexandrum* in Jammu and Kashmir is expected to be severely affected by the changing climatic scenarios, losing most of its suitable habitats in the Kashmir Valley. The intensity of the habitat loss in Jammu and Kashmir increases with the extremity of the climatic scenarios, with losses of 3.92%, 4.06% and 18.67% under SSP126, SSP370 and SSP585 pathways, respectively. This may be due to the projected warmer climates and a decrease in precipitation under future scenarios, leading to an overall shift toward drier regimes in the Kashmir Himalaya[55]. Uttarakhand is expected to lose some of its suitable habitats under extreme scenarios, but many areas that are currently unsuitable for the plant are predicted to become suitable in future, more specifically under SSP126 pathway. Suitability of *P. hexandrum* is expected not to be severely affected under future climatic scenarios in Himachal Pradesh, with overall increase in the percentage of suitable habitats under optimistic as well as pessimistic scenarios (Fig. 9). However, the species is expected to undergo a significant range change. Under future climatic scenarios, *P. hexandrum* is predicted to shift southeastwards more drastically under pessimistic scenarios, which may signify a reaction to water availability instead of temperature alterations. Similar southeastward shifts have been predicted for *Bergenia ciliata* and *Bergenia stracheyi*, mid-altitudinal and high altitudinal plant species, respectively, of the Himalayan region[56].

Our model predicts the distribution of *P. hexandrum* within some protected areas of the western Himalayas. *P. hexandrum* has been reported from the Valley of Flowers, Nanda Devi Biosphere Reserve, The Great Himalayan National Park, Gulmarg Wildlife Sanctuary and Overa Aru Wildlife sanctuary[57–61]. Overlapping of the suitable habitats of *P. hexandrum* with Protected Area Networks may play an important role in its conservation, provided these protected areas are well managed to offer quality habitats for the species[62]. However, the decline in the number of individual plants due to habitat fragmentation, low rate of natural regeneration or seed germination, and prolonged dormancy has been the major factor causing a decrease in the size of its wild populations[63,64]. *P. hexandrum* has a very small population in the Himalayas (40–700 plants per location), and it is declining every year due to overexploitation and anthropogenic activities[38,65,66]. Furthermore, its survival is threatened by inadequate regeneration and the rising demand for podophyllotoxin, which is found in its rhizome[67]. Despite periodic conservation efforts, including its 1987 designation as endangered in India[68], the prohibition on export of the species and its derivatives under Schedule 2-Appendix 2 of the Export and Import Policy 1997–2002[69], and Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora[70], the population of *P. hexandrum* continues to decline, and the species is currently listed as globally "Endangered" in the IUCN Red List of Species[38]. There is currently no indication that existing legal protections and bans on wild collection are sufficient to reverse or even stabilize the declining trend. Without more robust enforcement, community-based conservation, cultivation initiatives, and habitat protection, harvest levels are expected to remain at unsustainably high levels. A multifaceted conservation approach, combining policy reinforcement with active ecological management, is urgently required to ensure the survival of this ecologically and medicinally important species. Existing natural populations of *P. hexandrum* need to be protected through strengthening of Protected Area Networks within its distribution range. Strict enforcement of anti-harvesting regulations, ecological monitoring, and restoration of degraded habitats is critical. Furthermore, assisted migration could be explored cautiously as a future-oriented strategy to facilitate the species' establishment in climatically suitable but currently unoccupied regions. These integrated efforts will be vital for maintaining the long-term viability of this ecologically and medicinally valuable species. Community-based conservation programs involving local stakeholders in sustainable management practices and awareness campaigns can also enhance its conservation.

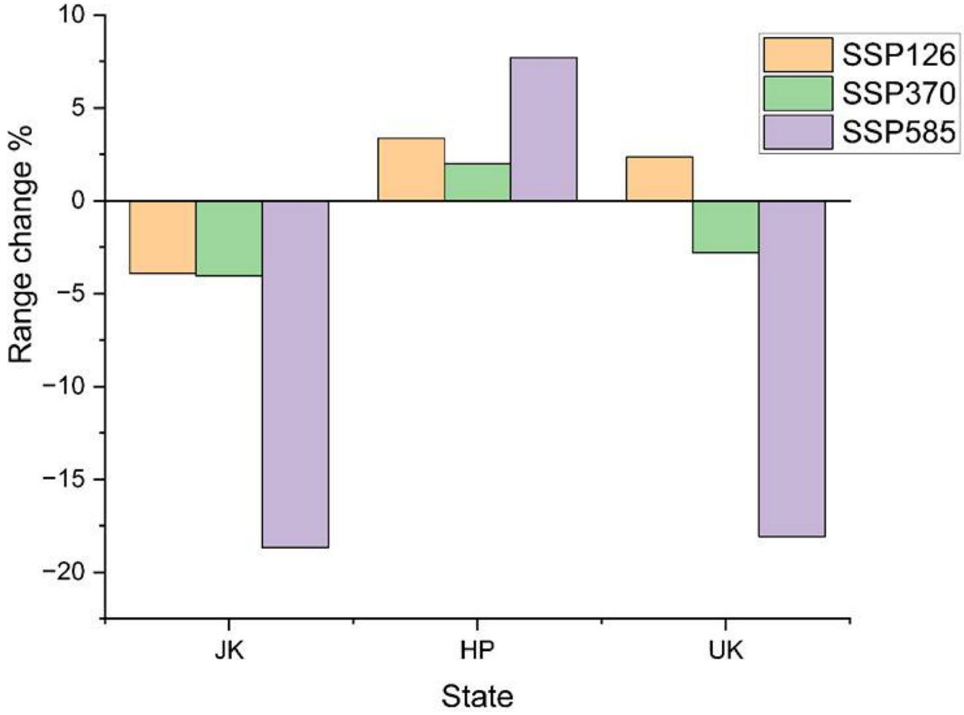

Fig. 9. State wise range change dynamics in the distribution of *Podophyllum hexandrum* under future climatic scenarios with respect to the current climatic conditions (JK = Jammu and Kashmir including Ladakh; HP = Himachal Pradesh; UK = Uttarakhand).

Promotion of large-scale cultivation under controlled conditions can reduce pressure on wild populations while supporting the pharmaceutical demand for podophyllotoxin. Research aimed at optimizing germination protocols and propagation techniques is also vital for effective reintroduction and restoration initiatives in the future.

Novelty and limitations of the study

This study is the first to model the potential distribution of *P. hexandrum* using CMIP6-based SSPs, thereby offering improved climate projections over earlier studies that relied on CMIP5 scenarios. Additionally, instead of using the more commonly applied WorldClim dataset, this study utilizes CHELSA climatic variables, which offer higher accuracy in complex mountainous terrains such as the Himalayas due to their inclusion of orographic effects[71]. A novel aspect of this research is the explicit quantification of centroid shifts and migration distances under future climate scenarios, providing valuable insights into spatial redistribution trends. Collectively, these methodological innovations make the study a significant step forward in understanding and safeguarding the future of this ecologically and medicinally important species. However, the focus of this study was to assess the potential distribution of *P. hexandrum* under current and future climate change scenarios; therefore, only climatic variables were used to predict the suitable habitats. Other variables, such as, topographic, edaphic and biotic variables were not explicitly incorporated into the species distribution models. The exclusion of these interactions could lead to over- or underestimation of suitable habitats, especially in ecologically complex regions like the Himalayas. Thus, future research should consider integrating these variables along with climatic variables to enhance ecological realism and predictive accuracy. Additionally, in the present study future projections were limited to a single time period (2041–2070). Incorporating near-future (2030) and far-future (2090) time periods would provide a more comprehensive understanding of species responses across short, medium, and long-term climate scenarios, thereby supporting more effective monitoring and conservation planning.

Conclusion

Podophyllum hexandrum is an important medicinal plant of the Himalayan region that has recently been categorized as endangered. The plant species is facing severe survival challenges owing to its poor regeneration, and overexploitation coupled with climate change. In the present study, habitat suitability modelling of *P. hexandrum* was carried out to identify its potentially suitable habitats under current and future climatic scenarios. *P. hexandrum* is considered intolerant to dry conditions, and in the Himalayan region fluctuating water availability and increased water deficit are anticipated to induce drought-like conditions, threatening its survival under future climatic scenarios. Our model predicted that *P. hexandrum* will undergo severe range changes under future climate change scenarios and will lose most of its currently suitable habitats. Though, the overlap of suitable habitats of *P. hexandrum* with Protected Area Networks plays an important role in the conservation of its wild populations, the decline in the number of individuals due to habitat fragmentation, low rate of natural regeneration or seed germination and prolonged dormancy is a serious concern. Thus, there is an urgent need to develop pertinent conservation and management policies for habitat restoration and reintroduction of this species. Protocols should be standardized for mass multiplication of *P. hexandrum* through seeds and tissue culture and the predicted suitable habitats in the present study will serve as baseline information for the possible introduction of *P. hexandrum* in potentially suitable habitats. Raising awareness and building the capacity of local communities for sustainable harvesting and involving them in the conservation of *P. hexandrum* may ensure long-term conservation of the species.

Data availability
All data generated or analyzed during this study are included in this published article.

Received: 4 February 2025; Accepted: 7 July 2025
Published online: 14 July 2025

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Acknowledgements
Zishan Ahmad Wani acknowledges the Department of Environmental Science and Engineering, SRM University-AP for providing University Post Doctoral Fellowship.

Author contributions

Z.AW. Conceptualization, Data collection, Data analysis, Z.A.W. and P.P.A.R. wrote the main manuscript and prepared figures. J.A.D. Supervision. J.A.D., A.N.L. and S.S. reviewed and edited the manuscript. S.S. Funding acquisition. All authors reviewed the manuscript.

Funding

The authors extend their appreciation to the Deanship of Research and Graduate Studies at King Khalid University for funding this work through Large Group Project under grant number RGP2/89/46.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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