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Author for Correspondence: Dr Irfan Rashid, Email: irfanrashid@uok.edu.in

Differential responses of Kashmir Himalayan threatened medicinal plants to anticipated climate change

Javaid M Dad and Irfan Rashid

Department of Botany, University of Kashmir, Srinagar – 190 006, Jammu and Kashmir, India

Summary

As natural and anthropogenic forcings impel anticipated climate change, their effects on biodiversity and environmental sustainability are evident. A fundamental question that is often overlooked is: which changes in climate will cause the redistribution or extinction of threatened species? Here, we mapped and modelled the current and future geographical distributions of the four threatened medicinal plants – *Aconitum heterophyllum* Wall. ex Royle, *Fritillaria cirrhosa* D. Don, *Meconopsis aculeata* Royle and *Rheum webbianum* Royle – in Kashmir Himalaya using maximum entropy (MaxEnt) modelling. Species occurrence records were collated from detailed field studies carried out between the years 2010 and 2020. Four general circulation models for Representative Concentration Pathway (RCP) 4.5 and RCP8.5 climate change scenarios were chosen for future range changes over periods around 2050 (average for 2041–2060) and 2070 (average of 2061–2080). Notable differences existed between species in their responses to predictive environmental variables of temperature and precipitation. Increase in the most suitable habitat, except for *A. heterophyllum* and *R. webbianum*, were evident across Himalayan Mountain regions, while the Pir Panjal mountain region exhibited a decrease for all four species under future climate change scenarios. This study exemplifies the idiosyncratic response of narrow-range plants to expected future climate change and highlights conservation implications.

Introduction

Biological diversity represents a significant livelihood option for human survival (IPBES 2019). Although reducing global biodiversity loss and halting species extinction are central to the Convention on Biological Diversity and United Nations Sustainable Development Goals, success to date has been extremely limited (United Nations 2015). The lists of species facing extinction threats have increased exponentially over the past several decades. To develop effective conservation strategies, particularly for already listed rare, endangered and threatened (RET) species, background knowledge regarding their distribution and predicting their habitat suitability under a changing climate is highly important (Marcer et al. 2013, Megan 2021). Thus, the use of technology in generating climate scenarios and potential species distributions for current and future climate scenarios has increased manifold (Terribile et al. 2009, Mouquet et al. 2015). Species distribution models (SDMs) are extremely helpful for studying niche specificity and species' responses to climate change (Yi et al. 2014) and for optimizing protection networks for climate change adaptation by identifying target areas highly suitable for the reintroduction or rehabilitation of species (Fois et al. 2016). However, because SDMs vary hugely in predicting species distributions, unimodal SDM studies to produce projections are deemed superficial (Dyderski et al. 2018). Therefore, the application of an ensemble of projections from a range of climate models is highly preferred, particularly for the conservation planning of RET plants, where a range of climate change projections must be considered. Among various SDMs, the maximum entropy (MaxEnt) modelling approach is valuable for delineating species occurrence probabilities (Kaky et al. 2020) and, combined with ensemble projections from multiple general circulation models (GCMs), it is highly preferred because it minimizes the predictive uncertainty of single models (Knutti et al. 2017). Thus, using MaxEnt with multiple GCMs for mapping species distribution appears highly promising and helpful for conservation planning.

Kashmir Himalaya (KH) is a biodiversity hotspot that forms the north-western province of the Indian Himalayan Region (IHR). The most recent investigation of its floral biodiversity lists 1123 plant species used specifically for medicinal purposes (Tali et al. 2019). Amongst these, *Aconitum heterophyllum* Wall. Ex Royle (Ranunculaceae), commonly called Indian Atees (altitude 2800–4000 m), *Fritillaria cirrhosa* D. Don (Liliaceae), known as yellow Himalayan fritillary (altitude 2500–4200 m), *Meconopsis aculeata* Royle (Papaveraceae), called blue poppy (altitude 2500–4700 m), and *Rheum webbianum* Royle (Polygonaceae), known as Indian rhubarb (altitude 2600–4500 m), are found at higher altitudes in narrow pockets (Fig. 1). While *M. aculeata* is



Fig. 1. Four threatened medicinal plants in their natural habitats of Kashmir Himalaya.

endemic to KH, the other species have relatively extended distributions and are highly valued with known pharmacological properties (Paramanick et al. 2017, Cunningham et al. 2018, Bahukhandi et al. 2019). Of the total of 152 potential medicinal and aromatic plant (MAP) species reported from the region based on medicinal value, market demand, availability and uses in traditional herbal systems, *A. heterophyllum* and *F. cirrhosa* are included amongst 43 potential MAPs prioritized for cultivation and conservation in the Western Himalaya (Negi et al. 2018). However, overexploitation and unlawful trading of these species have put severe pressure on their natural populations and thus while *F. cirrhosa*, *M. aculeata* and *R. webbiana* are identified as endangered, critically endangered and vulnerable in the regional Conservation Assessment and Management Plan (CAMP 2003), *A. heterophyllum* (Fig. 1) is identified as globally endangered and listed under the International Union for Conservation of Nature (IUCN) Red List (Ved et al. 2015). Despite this, the earlier work across KH has mostly focused on the distribution and documentation of these plants' medicinal uses (Dad & Khan 2011, Tali et al. 2014). However, given the projection that by the end of twenty-first century the region in its average annual temperature might witness an increase of between 3.98°C and 6.93°C under Representative Concentration Pathway (RCP) 4.5 and RCP8.5 scenarios, respectively (Romshoo et al. 2020), the individual responses of these highly vulnerable species to anticipated climate change need to be known. Previous studies have demonstrated that changing climate will hugely impact vegetation distribution across KH, with severe impacts on grasslands and forest ecosystems (Rashid et al. 2015), but its effects on the distribution of MAPs have not been evaluated. As these plants exhibit distinct spatial patterns and are hugely influenced by

various environmental factors, we aimed to elucidate how key climate factors, including temperature and precipitation, influence the distribution of four medicinal plants, namely *A. heterophyllum*, *F. cirrhosa*, *M. aculeata* and *R. webbiana*, across KH, to understand their current distribution patterns and to predict their future distribution using an ensemble of four GCMs. Within a broader framework of devising long-term conservation strategies in KH, we discuss the implications for medicinal plant conservation across KH.

Materials and methods

Study area

KH stretches between 32°22'–34°43'N and 73°52'–75°42'E. Due to its fragile ecology, it is extremely sensitive to even minor climatic changes (Dad et al. 2021). The study area is covered with majestic mountain ranges, including the north-western Himalaya and the Pir Panjal range. Owing to the topographical and climatic contrasts, these mountain ranges hold a wide variety of natural ecosystems and grow plants that are highly prized in modern medicine. The climate, marked by well-defined seasonality, resembles that of mountainous and continental parts of temperate latitudes, with four seasons of summer (June–August), autumn (September–November), spring (March–May) and winter (December–February).

Species data

The primary source of the species occurrence data is our detailed fieldwork carried across the region between 2010 and 2020 (Dad & Khan 2011, Dad & Reshi 2015, Dad 2019). In addition, we also compiled the species location points from Kashmir University Herbarium (KASH) and other secondary sources such as the Global Biodiversity Information Facility (GBIF) database (<http://www.gbif.org>). However, in order to avoid autocorrelation and to enhance data credibility, the occurrence data were processed using ArcGIS 10.2.1. Then, using the SDM toolbox, the spatial autocorrelation of species distribution was checked and redundant presences were removed. A spatial thinning along 5 × 5 km grid cells was carried out to reduce model bias. Thus, of the totals of 47, 42, 31 and 41 occurrence records for *A. heterophyllum*, *F. cirrhosa*, *M. aculeata* and *R. webbiana*, respectively, only 36, 31, 28 and 30 rarefied points were used to generate SDMs.

Climate data

The climate data were downloaded and processed from WorldClim database version 1.4 (<http://www.worldclim.org/>). In total, 19 bioclimatic variables derived from monthly temperature and precipitation data and 1 topographic variable (elevation) were processed using ArcGIS 10.2.1 at a spatial resolution of 30 arc-seconds (c. 1 × 1 km; <https://www.worldclim.org/data/worldclim21.html>; <https://www.worldclim.org/data/v1.4/cmip5.html>). To avoid multicollinearity, Pearson's correlation coefficient was calculated for variable pairs using the ecological niche model toolbox, and variables exhibiting high multicollinearity (>0.7) were eliminated to ensure better model predictability (Supplementary Table S1, available online). Thus, the eight variables of annual mean temperature (°C; BIO1), mean diurnal range (maximum temp–minimum temp; °C; BIO2), temperature seasonality (SD × 100; %; BIO4), temperature annual range (BIO5 – BIO6; °C; BIO7), mean temperature of the wettest quarter (°C; BIO8), annual precipitation (mm;

Table 1. A statistical summary of the average estimates of the maximum entropy (MaxEnt) distribution models for four threatened medicinal plants across Kashmir Himalaya.

Species	Climate scenario		Summary statistics								
			MR _{TG} (%)	MUR _{TG} (%)	M _{TG}	MT _{AUC}	Mt _{AUC}	MAUC _{sd}	Cohen's κ	TSS	
<i>Aconitum heterophyllum</i>	Current			1.24	1.58	0.85	0.92	0.91	0.05	0.46	0.77
	Future projection	2050	RCP4.5	0.84	1.12	0.88	0.96	0.90	0.009	0.41	0.76
			RCP8.5	1.02	1.20	0.81	0.92	0.87	0.169	0.38	0.69
	Future projection	2070	RCP4.5	0.94	1.45	0.82	0.84	0.79	0.079	0.36	0.63
RCP8.5			0.85	1.14	0.83	0.96	0.92	0.029	0.47	0.77	
<i>Fritillaria cirrhosa</i>	Current			1.28	1.47	0.84	0.90	0.92	0.06	0.44	0.78
	Future projection	2050	RCP4.5	0.89	1.01	0.88	0.95	0.93	0.06	0.56	0.79
			RCP8.5	1.14	1.24	0.81	0.92	0.89	0.07	0.40	0.69
	Future projection	2070	RCP4.5	1.21	1.51	0.84	0.85	0.83	0.08	0.38	0.66
RCP8.5			0.87	1.02	0.82	0.94	0.91	0.07	0.43	0.77	
<i>Meconopsis aculeata</i>	Current			1.29	1.45	0.89	0.91	0.88	0.07	0.40	0.70
	Future projection	2050	RCP4.5	1.32	1.40	0.85	0.93	0.90	0.05	0.42	0.77
			RCP8.5	1.42	1.62	0.89	0.93	0.88	0.08	0.41	0.71
	Future projection	2070	RCP4.5	1.31	1.63	0.80	0.82	0.89	0.07	0.40	0.77
RCP8.5			1.26	1.36	0.92	0.94	0.91	0.04	0.47	0.75	
<i>Rheum webbianum</i>	Current			1.35	1.52	0.82	0.84	0.92	0.07	0.46	0.78
	Future projection	2050	RCP4.5	1.51	1.54	0.89	0.95	0.92	0.02	0.49	0.78
			RCP8.5	0.98	1.23	0.78	0.81	0.89	0.09	0.40	0.77
	Future projection	2070	RCP4.5	0.98	1.15	0.87	0.85	0.90	0.04	0.42	0.77
RCP8.5			1.11	1.42	0.89	0.90	0.89	0.06	0.40	0.78	

MR_{TG} = mean regularized training gain (%); MUR_{TG} = mean unregularized test gain (%); M_{TG} = mean test gain; MT_{AUC} = mean training area under the curve; Mt_{AUC} = mean test area under the curve; MAUC_{sd} = mean area under the curve standard deviation; TSS = true skill statistics; RCP = Representative Concentration Pathway.

BIO12), precipitation seasonality (unitless; BIO15) and elevation (metres above sea level; ELEVATION) were used for generating SDMs. The projected changes of species distribution were modelled to the years 2050 (average for 2041–2060) and 2070 (average for 2061–2080) under Representative Concentration Pathways (RCPs) 4.5 (Wise et al. 2009) and 8.5 (Riahi et al. 2011), which correspond to intermediate and high levels of global radiative forcing, respectively. For future climate change scenarios, bioclimatic variables from four GCMs were used: GFDL-CM3 (Griffies et al. 2011), MRI CGCM3 (Yukimoto et al. 2012), CNRM CM5 (Voldoire et al. 2013) and CCSM4 (Al-Qaddi et al. 2017). We calculated the multi-model ensemble mean of the four models with equal weight.

Model design

The model was run using the MaxEnt algorithm (version 3.4.1 k; Phillips et al. 2006). For model calibration, we used 75% of the data for training and 25% for testing. The models were run with 10 replicates, and model performance and accuracy were measured using the area under the curve (AUC) scores of the receiver operator characteristic (ROC), true skill statistics (TSS) and Cohen's κ (Fois et al. 2018). Amongst these, the ROC curve (AUC) represents the threshold-independent index while the TSS and Cohen's κ are the threshold-dependent indices, with TSS dealing with both sensitivity and specificity. The value of TSS ranges from -1 to +1, where +1 indicates perfect agreement while scores from 0.6 to 0.9 specify fair to good model performance (Allouche et al. 2006). Different regularization parameters such as mean regularized training gain, mean training AUC and mean test AUC were recorded to check model overfitting, while the relative importance of each predictor was measured using the percentage contribution of the jackknife test (Phillips et al. 2006). For response curves and projected percentage area change of species climatic niches, a distribution probability above 0.5 (Stockwell & Peterson 2002) was used. The habitat suitability map was converted into the suitable and unsuitable areas (Xu et al. 2019), and the potential suitable area

for each of the four species was calculated using the maximum training sensitivity plus specificity logistic threshold. The distribution map was then categorized into three main suitability classes, namely low, medium and high, with suitability values on a percentage basis being 25–50%, 50–75% and >75%, respectively. The mean number of cells among each class was calculated and recorded as square kilometres for each suitability class (Fielding & Bell 1997). The variables selected in the current final model were used for projecting the potential distribution into future scenarios for two RCPs of the four GCMs GFDL-CM3, MRI CGCM3, CCSM4 and CNRM CM5, and the potential distribution changes between the current and future climate for each species were calculated by comparing the suitability maps for each scenario.

Results

Model evaluation

Model performance for current and future scenarios was high for both training and test data across all species (Table 1). The model also performed satisfactorily on both calibration and evaluation for AUC, TSS and other statistical scores such as mean regularized training gain, mean training AUC and mean test AUC (Table 1), suggesting that species distributions were near accurate.

Significant explanatory variables and current habitat suitability

F. cirrhosa and *M. aculeata* displayed the highest sensitivity to temperature, with a mean temperature of the wettest quarter (BIO8) appearing particularly important and contributing 62.3% and 61.7%, respectively, to their habitat suitability (Table S2). For *A. heterophyllum* and *R. webbianum*, BIO8 and annual precipitation (BIO12) were equally important (Table S2). Variables with the highest mean permutation importance were BIO8 and temperature seasonality (BIO4) for *M. aculeata*, precipitation seasonality (BIO15) and BIO12 for *A. heterophyllum* and *F. cirrhosa*, and

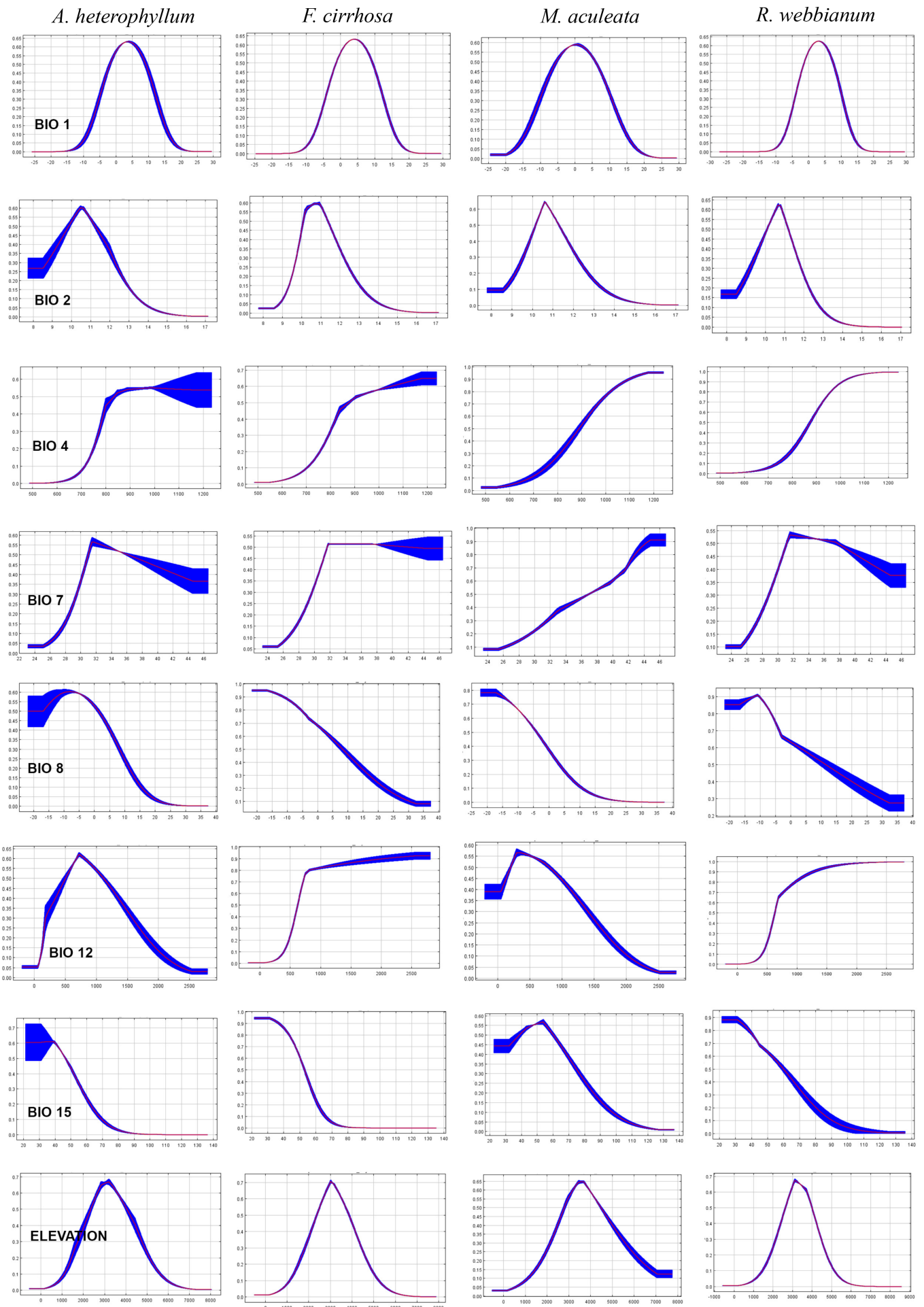


Fig. 2. Response curves of environmental predictors for four threatened medicinal plants species under the current climate scenario across Kashmir Himalaya. The x-axis of each graph represents the range of explanatory variables and the y-axis represents the probability of the presence of the species. For abbreviations, see the 'Climate data' section.

Table 2. Projected range changes (km²) for four threatened medicinal plants species under current and future climate change scenarios for 2050 and 2070 at two Representative Concentration Pathway (RCP) scenarios – RCP4.5 and RCP8.5 – categorizing low, medium and high suitability values as percentages of the total area of Kashmir Himalaya.

Species and distribution class	Current	Future scenarios			
		2050		2070	
		RCP4.5	RCP8.5	RCP4.5	RCP8.5
<i>Aconitum heterophyllum</i>					
Unsuitable	8348.9	13 856.3 (+65.9)	7916.6 (-5.2)	8117.6 (-2.8)	8432.9 (+1.1)
Low suitability	5728.1	1431.8 (-75.1)	6549.6 (+14.3)	5372.6 (-6.2)	5910.1 (+3.1)
Moderate suitability	1969.2	1159.9 (-41.1)	1716.5 (-12.8)	230.6 (-88.2)	2191.2 (+11.3)
High suitability	770.9	640.1 (-16.9)	634.8 (-17.7)	396.3 (-48.6)	282.1 (-63.4)
<i>Fritillaria cirrhosa</i>					
Unsuitable	9426.1	8783.9 (-6.8)	13 693.8 (+45.2)	15 783.8 (+68.4)	7782.3 (-17.4)
Low suitability	5072.9	6267.7 (+23.6)	1130.1 (-77.7)	269.9 (-94.7)	4991.7 (-1.6)
Moderate suitability	1924.5	1028.2 (-46.6)	2171.5 (+12.8)	200.2 (-89.5)	3142.9 (+63.3)
High suitability	487.6	782.9 (+60.5)	828.5 (+69.9)	573.3 (+17.6)	903.4 (+85.2)
<i>Meconopsis aculeata</i>					
Unsuitable	9372.1	8597.3 (-8.3)	12 926.5 (+37.9)	10 111.5 (+7.9)	15 633.8 (+66.8)
Low suitability	5570.4	4818.8 (-13.5)	2128.8 (-61.8)	3213.8 (-42.3)	444.7 (-92.0)
Moderate suitability	1358.6	2454.8 (+80.7)	824.7 (-39.3)	2596.8 (+91.1)	129.2 (-90.5)
High suitability	519.8	954.4 (+83.6)	941.4 (+81.1)	902.7 (+73.7)	619.8 (+19.2)
<i>Rheum webbianum</i>					
Unsuitable	12868.6	7134.4 (-44.5)	11 448.5 (-11.0)	9484.4 (-26.3)	14 053.8 (+9.2)
Low suitability	1287.1	6443.1 (+400.9)	3151.2 (+144.8)	4917.7 (+282.3)	1557.2 (+20.9)
Moderate suitability	1412.1	2486.6 (+76.1)	1499.1 (+6.2)	2054.7 (+45.5)	982.7 (-30.4)
High suitability	1258.4	757.8 (-39.8)	721.1 (-42.7)	359.2 (-71.5)	229.3 (-81.8)

For values in parentheses, '+' represents a gain and '-' represents a loss in range areas (in km²).

BIO12 and BIO4 for *R. webbianum* (Table S2). The response curves for BIO8 correlated negatively with species occurrences (Fig. 2). For BIO12, a skewed positive response was observed, with species showing high probabilities at annual precipitations >600 mm (Fig. 2). Similarly, *A. heterophyllum* and *F. cirrhosa* exhibited the highest probabilities at the lowest precipitation seasonality. However, for *M. aculeata* and *R. webbianum*, the occurrences were more frequent towards high-temperature seasonality and vice versa (Fig. 2). Notable differences existed between species in their responses to BIO8 and BIO12, and their probabilities exhibited a downwards trend at -3°C, 0°C, 2°C and 5°C and at 750, 500, 600 and 760 mm for *F. cirrhosa*, *M. aculeata*, *R. webbianum* and *A. heterophyllum*, respectively (Fig. 2). By contrast, the occurrence probabilities were seemingly similar for BIO4 for *M. aculeata* and *R. webbianum* (Fig. 2). Topographically, the mid-elevation range from c. 2200 to 4200 m was more suitable for all species, with an increased probability of presence recorded at elevations >3200 m.

Under the current climate, the habitat suitability model delineated and exhibited the predominance of the highest suitability habitat (HSH) for the assessed species in the highlands across KH: elevation ranging from 2200 to 4200 m. Under the current climatic scenario, 4.6%, 2.9%, 3.1% and 7.5% of the study area were highly suitable for *A. heterophyllum*, *R. webbianum*, *F. cirrhosa* and *M. aculeata*, respectively, which corresponds to c. 770.9, 487.6, 519.8 and 1258.4 km² (Table 2). Coincident with actual distribution, these HSHs are located mostly in the Himalayan Mountain system that runs in parallel to the direction of the Kashmir Valley and includes mountain ranges around Harmukh, Baltal, Chandanwari and Kholai, while a few HSHs (e.g., Affarwat and Ashtor) are also located in the Pir Panjal Mountain Range that spreads from Affarwat through Gulmarg to Banihal Pass (Fig. 3). On both mountain ranges, these HSHs primarily represent high-altitude ecosystems, including forests and grasslands.

Potential suitable distribution under future climate scenarios

The AUC values for potential suitable distribution under future climate scenarios were >0.8, indicating that model projections were satisfactory. The projected distribution showed different species behaving differently in each scenario (Figs S1–S4). While *A. heterophyllum* and *R. webbianum* recorded a steady reduction in their high potential habitat (HPH) (Figs S1 & S2), *M. aculeata* and *F. cirrhosa* exhibited an increasing percentage in their HPHs (Figs S3 & S4). The results revealed that by 2050 *A. heterophyllum* would lose 16.9% and 39.8% and *R. webbianum* would lose 17.7% and 42.7% of their current HPHs under RCP4.5 and RCP8.5, respectively, while by 2070 the decrease would be 48.6% and 71.5% for *A. heterophyllum* and 63.4% and 81.8% for *R. webbianum* under RCP 4.5 and RCP8.5, respectively. However, *F. cirrhosa* and *M. aculeata* were projected to gain for both RCP4.5 and RCP8.5 (Table 3), with HSHs for *F. cirrhosa* increasing by 60.5% and 17.6% under RCP4.5 and RCP8.5, respectively, by the 2050s, and by the 2070s the corresponding increases would be 69.9% and 85.2%, respectively. In comparison, *M. aculeata* by the 2050s would increase by 83.6% and 81.1% under RCP 4.5 and RCP8.5, respectively, while by the 2070s the projected increases would 73.7% and 19.2% under RCP4.5 and RCP8.5, respectively (Table 3). However, despite differences in habitat loss and gain under different scenarios, the gain of new HSHs was evident across the Himalayan region, while the loss was across the Pir Panjal mountain range (Figs S1–S4).

Discussion

The primary aims of the present study was to elucidate how key climate factors, including temperature and precipitation, influence the distribution of the four medicinal plants *A. heterophyllum*, *F. cirrhosa*, *M. aculeata* and *R. webbianum* across KH, to

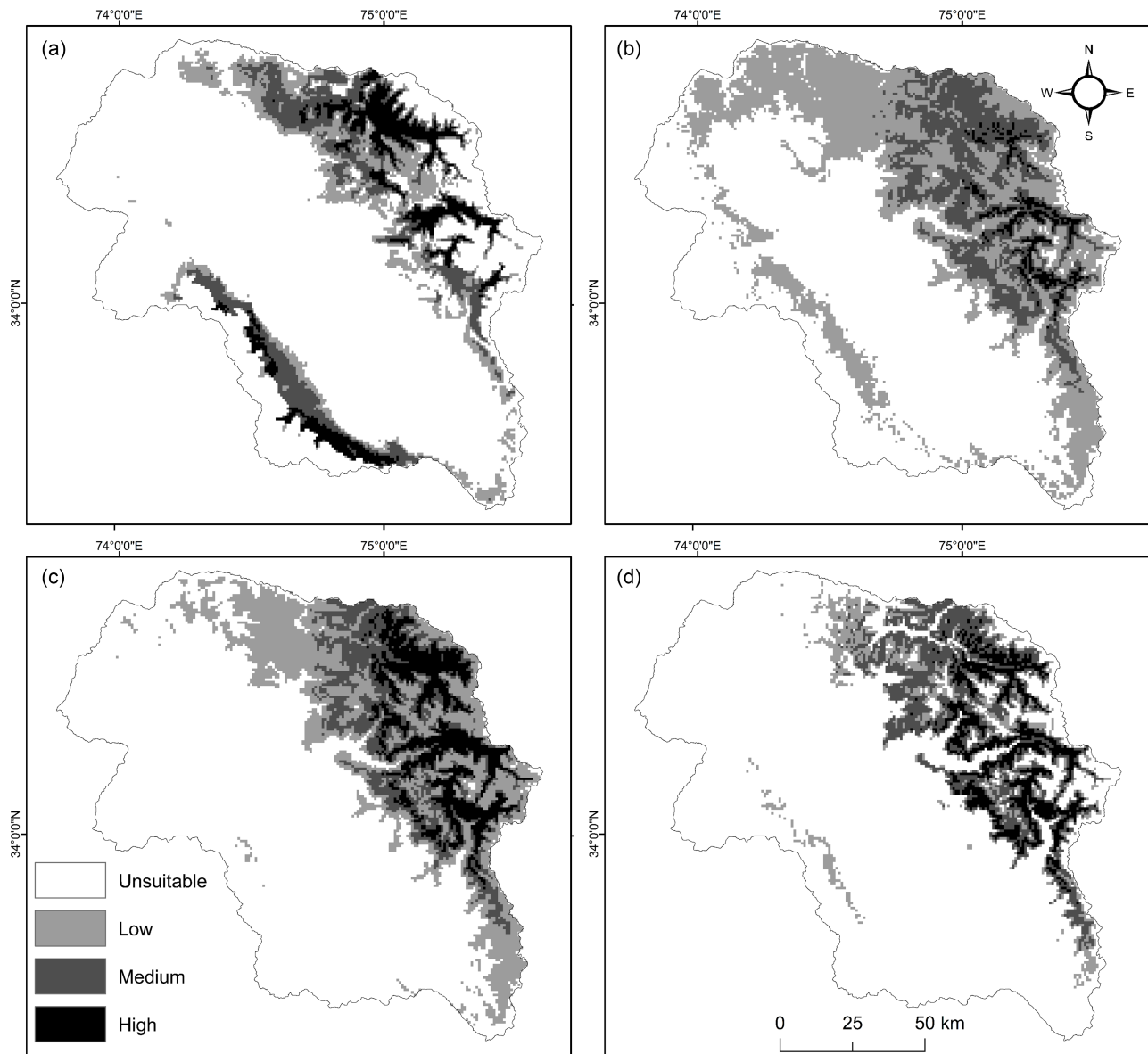


Fig. 3. Potential habitat distribution map for (a) *Aconitum heterophyllum*, (b) *Fritillaria cirrhosa*, (c) *Meconopsis aculeata* and (d) *Rheum webbianum* under the current climate scenario across Kashmir Himalaya. The three main suitability classes (i.e., low, medium and high) have suitability values of 25–50%, 50–75% and >75% on a percentage basis, respectively.

understand their current distribution patterns and to predict their future distributions using an ensemble of four GCMs. The bioclimatic variables adequately clarified the current distributions of the four medicinal plants across KH and, in agreement with previous studies, indicated that the habitat suitability and climate optima of these species lie at higher elevations (Gaira et al. 2011), where they grow under higher precipitation and colder temperatures in grasslands, forests and other alpine ecosystems (Dad 2019). The species' responses to predictive variables (Fig. 2) further supports this observation, corroborating reports that high-altitude, narrow-range species show greater preference towards certain temperatures and precipitation rates (Vincet et al. 2020). Under the current climate, the present study reveals that temperature-related variables rather than precipitation were more significant for *F. cirrhosa* and *M. aculeata*. Both temperature and precipitation were important for *A. heterophyllum* and *R. webbianum* (Table S2). Rana et al.

(2020) also reported similar results for six threatened MAPs across Nepal and opined that any change in the range value of predictive variables affects species probability presence (SPP). For the present study as well, the SPP approached zero at BIO8 >0°C or BIO12 <500 mm (Fig. 2), while it increased steadily as either BIO8 decreased or BIO12 increased. As these species prefer harsh winters with reasonable precipitation (Rana et al. 2017), the present study also demonstrated that these species prefer altitudes above 3000 m (Fig. 2), where winter temperatures are generally low. Jeelani et al. (2015) reported that, in response to specific ecological environments, high-altitude, narrow-range species develop phenotypic plasticity that helps them to adapt and establish at higher altitudes.

Although its discriminatory capacity makes the AUC the most widely used measure in SDM, AUC values generally tend to be higher for narrow-range species (Phillips et al. 2006). Therefore,

Table 3. Projected suitable areas of four threatened medicinal plants under current and future climate change scenarios for 2050 and 2070 at two Representative Concentration Pathway (RCP) scenarios – RCP4.5 and RCP8.5 – categorizing low, medium and high suitability values as percentages of the total area of Kashmir Himalaya.

Species	Future scenarios																	
	Suitability level ^a						2050						2070					
	Current suitable area (km ²)	Low (25–50%)	Medium (50–75%)	High (>75%)	Low (25–50%)	High (>75%)	Low (25–50%)	Medium (50–75%)	High (>75%)	Low (25–50%)	Medium (50–75%)	High (>75%)	Low (25–50%)	Medium (50–75%)	High (>75%)			
<i>Aconitum heterophyllum</i>	770.9	34.1	11.7	4.6	8.5	38.9	10.2	3.7	31.9	1.3	2.3	35.1	13.0	1.7				
<i>Fritillaria cirrhosa</i>	487.6	30.1	11.4	2.9	37.2	6.7	12.9	4.9	1.6	1.2	3.4	29.7	18.6	5.4				
<i>Mecranopsis aculeata</i>	519.8	33.1	8.1	3.1	28.6	12.7	4.9	5.6	19.1	15.4	5.4	2.6	0.8	3.7				
<i>Rheum webbianum</i>	1258.4	7.6	8.4	7.5	38.3	18.7	8.9	4.2	29.2	12.2	2.1	9.2	5.8	1.4				

^aSuitability level (%) is calculated out of the total area of the Kashmir Valley.

many studies criticize putting the AUC as the best model criterion (Peterson et al. 2008) and advocate for its use in situations involving true instance of species absences (Jiménez-Valverde 2012). Thus, comparing AUC values between species seems unsteady. But as we used AUC values as part of multiple assessment indices (AUC, TSS and Cohen’s κ) together with detailed summary statistics such as mean regularized training and test gain (%), mean test gain and mean test AUC (Table 1), we deem it fit to report the AUC as a model accuracy measure for the present study. Consequently, the distribution maps generated using multiple GCMs delineating the climatic space of four threatened plants in the present study are in agreement with species’ actual distributions across KH. Moreover, as this study entailed geographical distributions on an adequate field-based dataset that ranks highly for SDMs of narrow-range species (Wisiz et al. 2008), this represents a significant enhancement over traditional distribution datasets. This study offers broader scope for practical conservation planning and sustainable management (Figs S1–S4).

Climate change is one of the five most important threats to global biodiversity (Nunez et al. 2019). Within a broader consensus that plant responses to climate change are highly variable (Zhao et al. 2018), it is argued that wide-niche species may adapt more effectively than narrow-niche species (Abolmaali et al. 2018). The results of the present study indicate that responses might differ between narrow-niche species. Thus, while changing precipitation and temperature regimes may not suit *A. heterophyllum* and *R. webbianum* and may lead to their shrinkage (Figs S1 & S2), they may match the requirements of *F. cirrhosa* and *M. aculeata* and lead to their expansion (Figs S3 & S4). Given that narrow-range species have lower genetic diversity levels than widespread congeners (Mateu-Andrés 2004) and are highly susceptible to drift (Boroń et al. 2011), the projected habitat shrinkage for *A. heterophyllum* and *R. webbianum* has profound conservation implications. In contrast, the projected expansion distribution for *F. cirrhosa* and *M. aculeata* indicates that these species may be introduced to a larger area in the future. However, as their expansion is based on models that lacked non-biotic interactions and dispersal capacities that may limit future species distributions (Morgan & Venn 2017), their ability to gain new HSHs must be interpreted with caution (Figs S3 & S4).

Considering the differences in predictive influences between current and future climate scenarios, the species differed greatly, with the differences observed being large for *A. heterophyllum* and *R. webbianum* and lower for *F. cirrhosa* (Table S3). For example, instead of BIO12 under the current climate, BIO2 and BIO4 appear to be highly important for *A. heterophyllum* and *R. webbianum*, while for *F. cirrhosa* the critical factors involve BIO4, BIO2 and BIO7, and for *M. aculeata* the predictive variables between current and future scenario differ only a little (Table S3). These differences indicate that in future, while temperature-related variables would appear favourable for *F. cirrhosa* and *M. aculeata*, the climatic space of *A. heterophyllum* and *R. webbianum* as influenced by increasing temperature and decreasing precipitation will be less suitable. Thus, we hypothesize that a shift in bioclimatic zone due to both temperature and precipitation will lead to a decline in the suitability of plant species across KH.

For area shrinkage and the expansion of HPHs, RCP4.5 represents the lower while RCP8.5 represents the higher distribution end. Thus, RCP8.5 appears to be most severe for *A. heterophyllum* and *R. webbianum*; RCP4.5 in the 2050s and 2070s appears favourable for *M. aculeata*, while RCP8.5 in the 2050s and 2070s appears favourable for *F. cirrhosa* (Figs S5–S8). For other species, previous

studies also predicted RCP4.5 as a favourable scenario in China (Gao et al. 2013), while for Himalaya, RCP8.5 is reported as favourable for habitat expansion (Rathore et al. 2019). Independent of the climate scenario, the present study projected habitat expansion mostly across the Himalayan Mountain range and shrinkage over the Pir Panjal range (Figs S5–S8). However, as the climatic space of all species seems to overlap in the Himalayan Mountain range, it would be a feasible space for both *in situ* and *ex situ* climate refugia. In contrast, HPHs across the Pir Panjal range would mainly serve for *in situ* climate refugia areas (Baumgartner et al. 2018). As anthropic pressures in most ecosystems in the elevation range of c. 3000–4000 m across KH have generally intensified (Dad 2019), the conservation of HPHs would benefit not only the species in question, but also other vulnerable species that lack adequate conservation. Particularly because this study has shown habitat shrinkage for species over the Pir Panjal range, the focus should be on initiating conservation measures across this range, and the results of the present study could aid in delineating conservation priority areas for optimizing protected area networks.

Conclusion

We mapped the geographical distribution of four threatened medicinal plants in KH and analysed projected changes under future climate scenarios. Our results show that the Himalayan Mountain region is of high importance for both current and future species distributions, while along the Pir Panjal mountain range the species would lose most of their suitable habitats. The habitat suitability showed range shifts through the disappearance of *A. heterophyllum* and *R. webbianum* and habitat expansion for *F. cirrhosa* and *M. aculeata*. Most importantly, while future temperature-related variables would appear favourable for *F. cirrhosa* and *M. aculeata*, the climatic space of *A. heterophyllum* and *R. webbianum* influenced by both increasing temperature and decreasing precipitation will be less suitable in the future. Thus, we hypothesize that a shift in bioclimatic zone triggered by both temperature and precipitation across KH will be the chief factor responsible for the decline in habitat suitability for these plants in the future. Given the differing behaviours of species to future climate change, target-based conservation, focusing on areas crucial for maintaining current species' populations and areas that are predicted to be essential under future climate change, is recommended.

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