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Original Research Article

Climate models predict a divergent future for the medicinal tree *Boswellia serrata* Roxb. in India



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ABSTRACT

Predicting the distribution of future climatically suitable habitat areas is crucial for the long-term success of species conservation and management plans. However, generating accurate predictions may be difficult as the assumptions and variables used in the construction of different climate scenarios may result in divergent trajectories of change. Nevertheless, generating species distribution models under multiple scenarios is helpful in selecting an optimal solution for practical applications. In this study, we compare the current distribution of climatically suitable areas of a threatened medicinally important tree, Boswellia serrata Roxb. in India with its distribution in the year 2050 modeled using two climate change scenarios - IPSL-CM5A-LR and NIMR-HADGEM2-AO - each represented by four representative concentration pathways (RCPs). Maximum entropy modeling with 19 bioclimatic variables was used to construct the climatic niche of B. serrata for predictions of present and future climatically suitable areas within India. The study revealed that annual mean temperature, mean temperature of wettest quarter and driest quarter, precipitation seasonality, and precipitation of wettest quarter potentially influence the distribution of the species. After thresholding, the model showed that ~21.95% of the geographical area in India is presently climatically suitable for the species. The IPSL-CM5A-LR and NIMR-HADGEM2-AO climate models revealed contrasting distribution scenarios of climatically suitable areas in India. However, irrespective of these climate models, the four RCPs predict a consistent decrease in suitable area with increases in climatic harshness. Substantial area in peninsular India is expected to lose climatic suitability in 2050, though new areas are also predicted to become climatically suitable. We suggest long-term conservation strategies for B. serrata be prioritized within future areas that are projected to retain climatic suitability.

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1. Introduction

Comprising ~12,235 species globally, medicinal plants contribute immensely to human livelihood, economy, culture, and medicine (Wiersema and León, 2016), with over 70% of the human population in developing countries depending on them for their primary healthcare needs (WHO, 2011). In addition to biological invasion, habitat degradation, and overextraction of biological resources, climate change continues to be a key factor threatening global and medicinal plant diversity (Barnosky et al., 2011; Dubey et al., 2018, 2019). Climate can have a dominating effect on ecological and biotic factors which may govern the geographic distribution of habitats and associated species (Ackerly et al., 2010; Dar et al., 2019). Changes in regional or global climate may therefore lead to local or global species extinction events (Bellard et al., 2012). The causal mechanisms that drive such extinctions are (i) altered plant-pollinator relationships that result from shifts in species phenology, and (ii) regeneration failure resulting from severe environmental stress on species and their natural habitats (Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Reyer et al., 2013). Studying the distribution of climatically suitable areas under future climate change scenarios is a crucial step in developing long-term conservation management strategies for threatened and economically important species (Ashrafzadeh et al., 2019), While projections of future climate change have been largely accepted by the global scientific community, there is ongoing debate regarding the trajectory of climatic change given the unpredictable nature of multiple influencing factors on future projections (Goberville et al., 2015). In this context, a plethora of climate models and scenarios have been developed by various scientific organizations, agencies, and groups across the globe for research, academic, and commercial purposes (http:// ccafs-climate.org/). As relying upon a single set of models or scenarios to predict future species distributions and inform policy decisions on conservation area prioritization can be risky, prioritizing climatically suitable areas with a consensus of current and future species distribution models generated using a wide range of climate scenarios may help to inform decisions when implementing long-term conservation plans. Following this approach, we tested two climate models using the case of Boswellia serrata Roxb. (Burseraceae) - a medicinally important deciduous tree species largely distributed throughout central and peninsular India (Bhutada et al., 2017; Wiersema and León, 2016). This species is under threat due to commercial harvesting for the extraction of medicinal and aromatic gum and resins for use in traditional ayurvedic medicines. Our objectives were to model and demarcate the present distributional range of B. serrata within India, and to predict climatically stable habitats in the event of future climate change using multiple projected climate scenarios.

2. Materials and methods

2.1. Species occurrences

We compiled 147 occurrence records of *B. serrata* from various regions of India from field surveys, online databases, and published literature. Of these, 104 GPS coordinates were recorded (accuracy \leq 10 m) by systematic field sampling undertaken in various parts of Central India covering the Satpura and Vindhyan mountain ranges in Madhya Pradesh from the year 2015–2017. An additional 29 records were downloaded from the online database of the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/occurrence/search?taxon_key = 5421354), and 14 were compiled from published literature (Table S1).

Table 1Description of 19 bioclimatic variables used (Source: O'Donnell and Ignizio, 2012).

Variable code	Description	Unit		
BIO1	Annual Mean Temperature	°C		
BIO2	Mean Diurnal Range (Mean of monthly (max temp — min temp))	°C		
BIO3	Isothermality (BIO2/BIO7) (*100)	%		
BIO4	Temperature Seasonality (standard deviation *100)	%		
BIO5	Max Temperature of Warmest Month	°C		
BIO6	Min Temperature of Coldest Month	°C		
BIO7	Annual Temperature Range (BIO5-BIO6)	°C		
BIO8	Mean Temperature of Wettest Quarter	°C		
BIO9	Mean Temperature of Driest Quarter	°C		
BIO10	Mean Temperature of Warmest Quarter	°C		
BIO11	Mean Temperature of Coldest Quarter	°C		
BIO12	Annual Precipitation	mm		
BIO13	Precipitation of Wettest Month	mm		
BIO14	Precipitation of Driest Month	mm		
BIO15	Precipitation Seasonality (Coefficient of Variation)	%		
BIO16	Precipitation of Wettest Quarter	mm		
BIO17	Precipitation of Driest Quarter	mm		
BIO18	Precipitation of Warmest Quarter	mm		
BIO19	Precipitation of Coldest Quarter	mm		

2.2. Bioclimatic predictors

The climatic niche of *B. serrata* was modeled using 19 bioclimatic variables (Table 1) that pertain to current and future, i.e. 2050s, conditions in India. These variables describe annual climatic temperature and precipitation trends, including seasonality and extremities-factors which may impose physiological constraints on species and affect their geographical distributions (O'Donnell and Ignizio, 2012). The bioclimatic variables for the current period are derivatives of the average monthly climate data for minimum, mean, and maximum temperature and precipitation of last 30 years, i.e. 1970-2000 (Fick and Hijmans, 2017). This dataset, with a spatial resolution of 2.5 min, was acquired in geoTiff format from the WorldClim website (http://worldclim.org/version2). For the future timeframe we selected two global general circulation climate models, IPSL-CM5A-LR (Dufresne et al., 2013) and NIMR-HADGEM2-AO (Baek et al., 2013), representing the average conditions for the period of 2041–2060. Each of these climate models are comprised of four Representative Concentrations Pathways (RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5), which are the standard scenarios of the IPCC Fifth Assessment Report (IPCC, 2014). The remaining variables used in the modeling were acquired from the website of the CGIAR Research Program on Climate Change, Agriculture, and Food Security (CCAFS) (http://ccafs-climate.org/). Considering the large geographical extent of India and use of secondary source occurrence data (~30% of the total records), we resampled all bioclimatic variables to a spatial resolution of 0.04° (~4 km) to match with the study design and saved them in ASCII raster format.

2.3. Ecological niche modeling

2.3.1. Model parameterization

Maxent software ver. 3.4.1 was used to model the climatic niche of *B. serrata* (Phillips et al., 2006). The model was parameterized using a maximum number of 10,000 background points, 500 iterations, and a convergence threshold of 0.00001. We used the hinge, product, linear, and quadratic feature types to deal with model complexity. Over-fitting was controlled using the default regularization value of one.

2.3.2. Evaluation of model performance

Model consistency was assessed using cross validations in MaxEnt by implementing 20 replicated model runs. The performance of the model was assessed based on the Area Under the Curve (AUC) value calculated by Maxent. The performance was also evaluated based on the partial AUC metrics (Lobo et al., 2008) calculated using the online tool Niche Toolbox (http://shiny.conabio.gob.mx:3838/nichetoolb2/). A distribution of AUC ratios was generated by executing 500 bootstrap simulations with 5% omission, followed by a statistical comparison of the means between AUC_{random} and AUC_{partial} to test whether the predictive model performed better than random expectations.

2.3.3. Assessing variable importance

The importance of the selected bioclimatic predictors was assessed based on analysis of variable contributions, jackknife procedure, and response curves. The analysis of variable contributions ranked the variables based on their relative contributions to the model gains. The jackknife procedure involved an iterative process where increases and decreases in the model gain were assessed after including or excluding one variable at a time from the analysis, while the response curves elucidated the influence of the variables in increasing the suitability across the climatic gradient.

2.3.4. Assessing novelty in future climate scenarios

Projecting niche models outside their calibration zone or climates may result in prediction errors due to the presence of one or more conditions whose range may be different from that of the calibration zone. Therefore, assessing environmental novelty in the projected climatically suitable areas or climates is crucial. We used the Multidimensional Environmental Similarity Surface (MESS) analysis option in MaxEnt to determine novel climatic conditions under future scenarios (Elith et al., 2011).

2.3.5. Predicting current and future distribution

The average 'Cloglog' outputs were converted to binary maps showing climatic suitability and unsuitability by employing a threshold rule of 10 percentile training presence. Here, the continuous suitability output is converted to a binary map in a manner such that 90% of the training records are included within the suitable range. Finally, climatic range shift scenarios were generated by intersecting the binary map of the current period with each of the future scenarios using Map Comparison Kit (Version 3.2; Visser and de Nijs, 2006). Each of these maps presents the following categories of potential priority areas for long term conservation: (i) retain suitability, (ii) gain suitability, (iii) lose suitability, and (iv) no suitability. Numerical data processing, analysis, and visualization were done using Microsoft Excel, while raster/vector data processing and mapping were done in ArcMap.

3. Results

3.1. Model calibration and performance

The average training and test AUCs were 0.959 ± 0.001 SD and 0.939 ± 0.043 SD respectively. The average partial AUC value at 5% omission was 0.938 with a standard deviation of 0.016 (Fig. 1). The high AUC values show satisfactory model performance.

3.2. Analysis of variable importance

The analysis of variable contributions showed that mean temperature of driest quarter (17.20%) had the highest rank followed by precipitation of wettest quarter (12.90%), precipitation seasonality (12.40%), and annual mean temperature (12.20%). These variables had a cumulative contribution of ~55% to the modeled potential climatic niche of *B. serrata* (Table 2). The jackknife analysis showed that the mean temperature of driest quarter contributed to the highest model gain (1.058) when used in isolation, while the mean temperature of wettest quarter decreased the overall gain the most (1.859) when it is omitted from the analysis (Table 2). This indicates that these variables may hold a significant influence compared to others and therefore have a role in species distribution.

Response curves for the most important variables reveal that the climatic niche of the species is characterized by an annual mean temperature of ~25 °C, mean temperature of wettest quarter of ~29 °C, mean temperature of driest quarter of ~30 °C, precipitation seasonality of ~14%, and precipitation of wettest quarter amounting to ~800 mm (Fig. S1). Thus, all identified variables provide an estimate of the important climatic attributes of the species niche and potentially influence the distribution of B. Serrata in India.

3.3. Current distribution of climatically suitable areas

The MaxEnt model predicted 21.95% of the total geographical area of India to be climatically suitable for *B. serrata* with a substantial area distributed in the states of Madhya Pradesh, Uttar Pradesh, Karnataka, Rajasthan, Maharashtra, Haryana, Chhattisgarh, and Jharkhand (Fig. 2, Table 3). A portion of the climatically suitable area also extended into the states of Uttarakhand, Gujarat, Tamil Nadu, Himachal Pradesh, Bihar, Punjab, Andhra Pradesh, Jammu & Kashmir, and Kerala (Table 3).

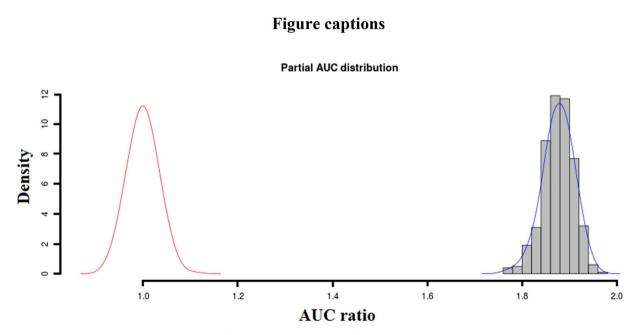


Fig. 1. Partial area under curve (AUC) ratio distribution for *Boswellia serrata* generated after 500 iterations with 5% omission in the receiver operating characteristic (ROC) space. Red curve show the distribution of AUC ratios for random models, while the blue curve along with shaded bars represents the frequency distribution of the ratios between AUC from model prediction and AUC random. Here, the significantly higher distributional range of AUC ratios indicates the better predictive ability of the model. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

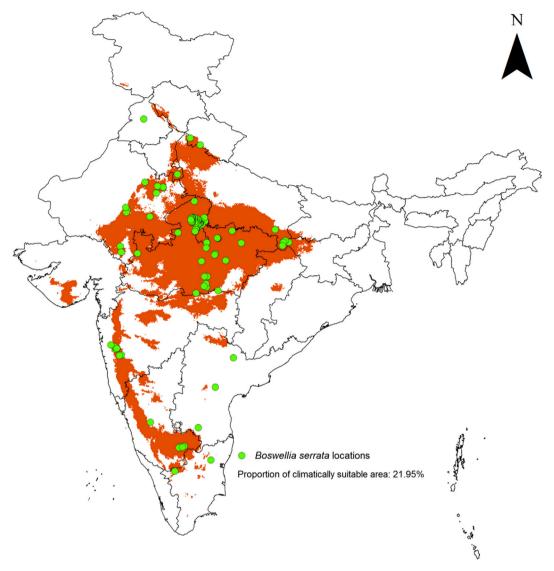


Fig. 2. Occurrence localities of *Boswellia serrata* overlaid on the modeled climatic suitability map of the species in India for current period. The shaded regions represent the climatically suitable area identified through applying ten percentile threshold limit to the average probabilistic output.

3.4. Distribution of future novel climates

The MESS analysis showed that substantial areas currently occupied by *B. serrata* populations in India may lack climatic novelty in the future. Nevertheless, areas that are expected to have novel climates in the future are mainly characterized by extreme ranges of annual mean temperature and mean temperature of coldest quarter (Figs. S2 and S3).

3.5. Effect of climate scenarios on future potential distribution areas

The IPSL-CM5A-LR and NIMR-HADGEM2-AO climate models predicted contrasting future potential distribution area extents for *B. serrata* in India (Fig. 3-5). The IPSL model predicted a substantial reduction in climatically suitable areas, ranging from ~7 to 14% of the total geographical area of India (Fig. S4) from the current value of 21.95% (Fig. 2), while the NIMR-HADGEM model predicted no major changes in total climatically suitable areas with ~21–22% compared to the current value (Fig. S5). The future potential distribution area showed a unimodal pattern across the RCP gradient in the case of the IPSL model, whereas the suitable areas showed a slight increase in RCPs 4.5 & 6.0. However, the NIMR-HADGEM model did not show a distinct trend.

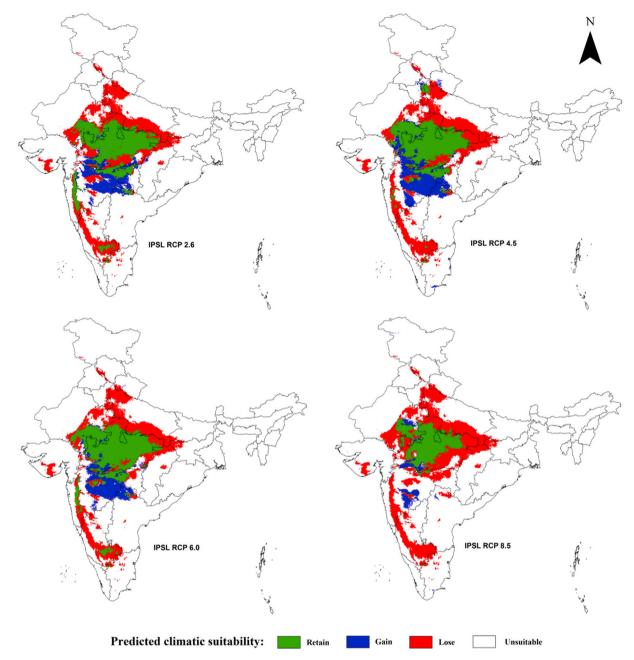


Fig. 3. Climatic range shift scenarios of *Boswellia serrata* in India developed after comparing the current distribution of climatically suitable areas with different RCPs of the IPSL-CM5A-LR climate model. Contrast of the future and present climatic suitability has been done keeping in view the following four possibilities i.e., gain suitability, lose suitability, retain suitability, and predicted as climatically unsuitable.

4. Discussion

In light of the influence of changing climate and loss of natural habitat on the decline of native plant populations, mapping potential species distribution areas through the use of predictive modelling tools can aid in the development of effective restoration and conservation management plans (Adhikari et al., 2012, 2018). Nevertheless, such tools potentially yield contrasting results due to inherent variation in the predictor variables of different sources, leading to confusion amongst end users as to the utility value of a given predictive distribution model. Conforming to this assumption, the MaxEnt models used in the present study, i.e. IPSL-CM5A-LR and NIMR-HADGEM2-AO climate models, revealed incongruous future distribution scenarios of *B. serrata* in India, where the former predicted a reduced future distribution while the distribution of the latter was relatively broader. Hence, we believe that completely relying on a single climate model for long-term conservation

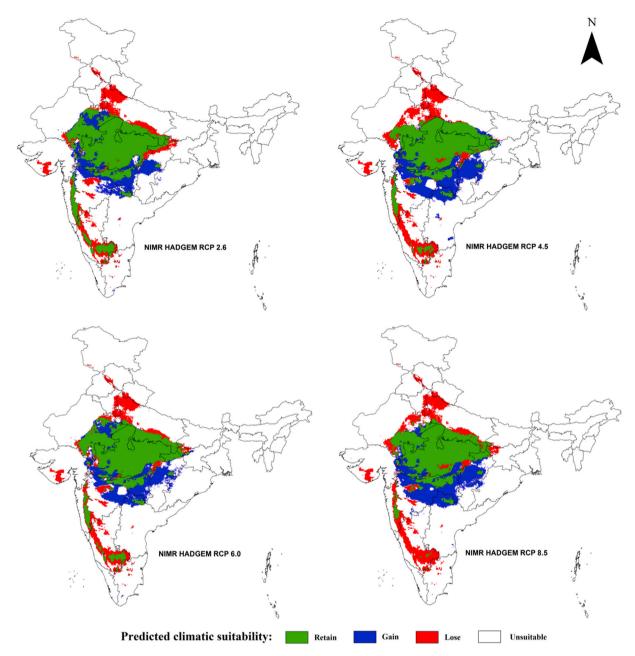


Fig. 4. Climatic range shift scenarios of *Boswellia serrata* in India developed after comparing the current distribution of climatically suitable areas with different RCPs of the NIMR-HADGEM2-AO climate model. Contrast of the future and present climatic suitability has been done keeping in view the following four possible outcomes i.e., gain suitability, lose suitability, retain suitability, and predicted as climatically unsuitable.

planning of threatened plants may be risky from a financial and logistical perspective. A more comprehensive approach that includes multiple climate models for this purpose may prove useful, providing an opportunity to draw a consensus that facilitates decision-making based on area prioritization (Beaumont et al., 2019).

Boswellia serrata is mostly distributed in the tropical dry deciduous forests of India and exhibit a variety of phenological responses related to vegetative and reproductive phases (Kushwaha et al., 2011). The species blossoms during the months of March—April and fruiting occurs during the winter season, i.e. during the months of November—December. These responses may represent survival strategies that have adapted in response to the variable monsoon bioclimatic conditions of India (Kushwaha et al., 2011). The MaxEnt models indicate that B. serrata is potentially sensitive to variation in the mean temperature of the driest and wettest quarter, precipitation of the wettest quarter, precipitation seasonality, and annual mean temperature. Particularly, the average climatic requirement of the species is characterized by an annual mean temperature of

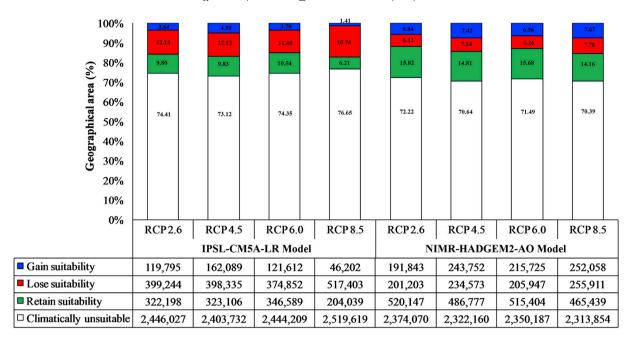


Fig. 5. Area statistics of the predicted shift in climatic ranges of *Boswellia serrata* in India under different RCPs of the two climate models namely IPSL-CM5A-LR and NIMR-HADGEM2-AO. The table shows the area (km²) covered under the four possible climatic outcomes. The numbers in the stacked bars represent the percentage area under each outcome.

Table 2Results of the analysis of variable contributions and Jackknife test of variable importance.

Bioclimatic variable codes	Analysis of variable contril	outions	Jackknife values of regularized training gain			
	Percent contribution	Permutation importance	Without variable	With only variable		
Bio 1	12.20	8.40	1.969	0.721		
Bio 2	2.00	1.50	1.962	0.602		
Bio 3	0.20	1.50	1.981	0.296		
Bio 4	3.20	2.70	1.973	0.664		
Bio 5	7.50	0.40	1.985	0.673		
Bio 6	0.20	0.80	1.985	0.671		
Bio 7	1.30	0.60	1.984	0.481		
Bio 8	5.50	16.50	1.859	0.582		
Bio 9	17.20	2.30	1.971	1.058		
Bio 10	5.90	13.20	1.934	0.610		
Bio 11	1.00	0.20	1.986	0.723		
Bio 12	5.60	17.60	1.973	0.746		
Bio 13	0.00	0.20	1.985	0.619		
Bio 14	0.60	3.10	1.970	0.046		
Bio 15	12.40	19.40	1.931	0.871		
Bio 16	12.90	7.10	1.974	0.651		
Bio 17	1.10	0.70	1.982	0.185		
Bio 18	7.40	0.90	1.982	0.371		
Bio 19	3.90	2.90	1.956	0.355		

~25 °C, mean temperature of wettest quarter of ~29 °C, mean temperature of driest quarter of ~30 °C, precipitation seasonality of ~14%, and precipitation of wettest quarter amounting to ~800 mm. A substantial deviation from these average conditions could profoundly impact the species' phenology and potential distribution. However, tree species can potentially adapt to altered environmental and climatic conditions by shifting their physiological and phenological behavior (Bellard et al., 2012). In this respect, this study provides a strong testable hypothesis regarding future experimental study into how different age classes of *B. serrata*, i.e. seedlings, saplings, and mature trees, would physiologically respond to altered temperature and moisture regimes.

Shrinking habitats, forest degradation, over-exploitation, changing climate, and soil conditions are major threats facing the native species of India. Intensive population assessment has shown a reduction in the distribution range of *B. Serrata* (Thakur and Khare, 2006). Over-exploitation for traditional medicines, soil-related changes, and grazing of saplings by fauna such as the Indian boar (*Sus scrofa cristatus*) have been attributed to changes in the regeneration of *B. serrata*. We propose that existing

Table 3Distribution of climatically suitable areas for *B. serrata* under different scenarios in India. The values in the shaded cells represent the proportion (%) of climatically suitable area in each state.

States	Geographical area	Climatically suitable area (%) in each state under different scenarios								
	(km ² x 1000)	Current	IPSL-CM5A-LR				NIMR-HADGEM2-AO			
			RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
Andaman and Nicobar	8.249	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Andhra Pradesh	275.045	2.88	6.95	9.11	7.30	0.38	7.54	13.92	9.23	12.04
Arunachal Pradesh	83.743	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Assam	78.438	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bihar	94.163	3.47	0.44	0.00	0.11	0.00	1.69	4.62	1.72	1.93
Chhattisgarh	135.192	14.30	3.50	0.61	3.59	0.00	30.05	54.21	43.16	55.02
Dadra Nagar Haveli	0.491	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Daman & Diu	0.111	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Delhi	1.483	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Goa	3.702	1.04	0.00	0.00	0.00	0.00	0,00	0.00	0.00	0,00
Gujarat	196.244	6.98	0.03	0.89	0.12	0.00	2.48	2.14	2.46	2.70
Haryana	44.212	20.57	0.00	10.91	0.00	0.00	0.04	0.00	0.00	0.00
Himachal Pradesh	55.673	5.03	0.00	0.27	0.00	0.00	0.15	0.27	0.00	0.00
Jammu and Kashmir	222.236	0.18	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Jharkhand	79.716	12.19	0.09	0.00	0.05	0.00	4.10	15.47	9.43	3.03
Karnataka	191.791	38.15	4.54	1.15	5.42	0.09	16.31	6.72	10.41	1.34
Kerala	38.852	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lakshwadeep	0.0326	0.00	0.00	0.00	0.00	0.00	0,00	0.00	0.00	0.00
Madhya Pradesh	308.252	87.40	69.08	72.12	76.39	52.45	95.30	94.58	95.09	95.88
Maharashtra	307.713	29.07	45.31	46.68	41.60	9.67	45.99	54.19	46.64	54.50
Manipur	22.327	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Meghalaya	22.429	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mizoram	21.081	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0,00
Nagaland	16.579	0.00	0.00	0.00	0.00	0.00	0,00	0.00	0.00	0.00
Odisha	155.707	0.00	0.00	0.00	0.00	0.00	0.43	3.38	2.76	2.67
Pondicherry	0.492	0.00	0.00	2.78	0.00	0.00	0.00	0.00	0.00	0.00
Punjab	50.362	3.34	0.00	0.26	0.00	0.00	0.10	0.00	0.00	0.00
Rajasthan	342.239	29.86	13.59	19.52	17.27	13.38	36.24	17.06	33.64	24.15
Sikkim	7.096	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tamil Nadu	130.06	6.74	1.00	2.06	0.63	0.58	2.94	1.64	2.64	0.41
Tripura	10.486	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Uttar Pradesh	240.928	43.63	4.82	6.14	4.52	3.83	19.58	26.91	23.04	20.83
Uttarakhand	53.483	7.78	0.00	3.78	0.58	0.00	0.00	0.00	0.00	0.00
West Bengal	88.752	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

and potential future habitats of *B. serrata* should be managed by formulating policies for limited regulated extraction, reduction of grazing impacts, and improvement of soils.

In the present study, both climate models revealed a distinct reduction and shift in the potential distributional range of *B. serrata* within India. These results correspond with numerous studies on the influence of climate change on the distribution ranges of plant species characterized by range shifts, expansions, and contractions (Allen, 2009; Early and Sax, 2014). Such shifts may have profound impacts on species survival and proliferation (Monteith et al., 2015). Anticipating these range shifts through the use of predictive modelling tools may help in identifying refugia for the long-term conservation of threatened species (Beaumont et al., 2019), through which conservation goals can be achieved. In the present study, we have identified such refugia for *B. serrata* within areas that are projected to either retain climatic suitability or become climatically suitable in the future and thus can provide a strong framework for the identification of refugia for other threatened species in India.

In India, policies relating to biodiversity conservation presently emphasize *in situ* and *ex situ* conservation measures including protected area delineation and management, habitat restoration, reduction of anthropogenic pressures, and rehabilitation of threatened species across their habitat range through biotechnological intervention. We believe that uncertainties in future climatic conditions should be properly explored, addressed, and accommodated in the policies and planning processes related to biodiversity conservation. Through this study, we demonstrate that niche-based analyses and a consensus of different climate models can help in identifying suitable areas and refugia for long-term conservation of threatened species and potentially improve the resilience of entire conservation networks by mitigating the impacts of habitat loss and fragmentation on biodiversity loss.

Declaration of competing interest

Authors declared no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01040.

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