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RESEARCH

How can dry tropical forests respond to climate change? Predictions for key Non-Timber Forest Product species show different trends in India

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Abstract The present study provides an assessment of the distribution of key Non-Timber Forest Product species in India, namely *Aegle marmelos* (L.) Correa, *Buchanania lanzan* Spreng., *Madhuca longifolia* (J. Koenig ex L.) J. F. Macbr., *Phyllanthus emblica* L. and *Terminalia bellirica* (Gaertn.) Roxb. The suitable habitat was analyzed under current climate scenarios and subsequently, the future distribution (2050s and 2070s) was mapped under RCP 2.6 and 8.5 scenarios, along with the past distribution (mid-Holocene, ~6000 cal year BP) using the MaxEnt species distribution model. The distribution of all species is primarily driven by key bioclimatic factors, including annual precipitation (Bio_12), mean annual temperature (Bio_1), isothermality (Bio_3) and precipitation of the coldest quarter (Bio_19). The results indicate that the present distribution of these species is mainly centred in the Western Ghats regions, Central Highlands, North-eastern India and Siwalik hills. The current study suggests that under the future climate change, the suitable habitat for *A. marmelos* and *T. bellirica* is expected to increase while for *B. lanzan*, *M. longifolia* and *P. emblica*, it is projected to decline. *A. marmelos* and *T. bellirica* are anticipated to exhibit resilience to future climate changes and are expected to be minimally affected, while *B. lanzan*, *M. longifolia* and *P. emblica* are highly sensitive to high temperature and alteration in rainfall pattern expected under future climate changes. The projections of habitat suitability areas can be used as a valuable foundation for developing conservation and restoration strategies aimed at alleviating the climate change impacts on NTFP species.

Keywords Climate change · NTFP species · MaxEnt · Suitable habitat · Fossil pollen · Conservation

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Introduction

Forests have consistently held a significant role in shaping the religious, political, economic, cultural and social aspects of indigenous communities worldwide. According to a 2016 estimate from the Food and Agriculture Organization (FAO), around 1.6 billion individuals worldwide rely directly on forest for sustenance and livelihoods. Tropical forests are documented as the most vulnerable and heavily impacted ecosystems (Areendran et al., 2020). India's forests, covering more than 21% of its geographical area, sustain 16% of the global population and 18% of the world's cattle population (FAO, 2009) and also generate two trillion rupees through the production of Non-Timber Forest Products (NTFPs).

NTFPs are natural resources, excluding timber, harvested from wild plant or animal species extracted from their natural state, modified or cultivated forested environments (Ros-Tonen, 2000). It is used by humans for a variety of purposes including food, fibre, fodder, domestic materials, traditional medicine, construction materials and agricultural amenities and is often associated with cultural practices (Chopra, 1993). They are used in homes, sold commercially and also hold importance in social, cultural, or religious contexts (Talukdar et al., 2021). Globally, over a billion individuals rely directly on forests for their means of living and the rest of the population, totalling six billion, derive various economic, social and environmental advantages from forests (Pandey et al., 2016). In India, NTFPs generate an annual income of approximately US$ 2.7 billion and account for 55% of total employment within the forestry sector. Furthermore, these resources contribute to 50% of forest revenues and 70% of income from forest-based exports (Chauhan et al., 2008; Shiva & Verma, 2002). NTFPs can provide a valuable source of supplemental food for rural communities and support their livelihoods (Rowhani et al., 2011; Sarmah et al., 2008). Climate change has impacted the forest ecosystems where NTFP tree thrives, altering habitats and distribution (Scheffers et al., 2016; Magry et al., 2023). Alteration in temperature and rainfall patterns can influence the growth and viability of NTFP species, leading to population declines (Magry et al., 2023). Communities depending on NTFPs for their economic and cultural needs may experience negative impacts (Shackleton & Shackleton, 2004).

Among the diverse array of NTFP species in India, there are five major species: *Aegle marmelos*, *Buchanania lanzan*, *Madhuca longifolia*, *Phyllanthus emblica* and *Terminalia bellirica*, all of which hold significant socio-cultural relevance. For example, *A. marmelos* is recognized for its medicinal properties and is used in Ayurvedic medicine to treat various ailments (Singh & Bhatnagar, 2019). *B. lanzan* is utilized in culinary practices, offering sweet and acidic flavours as a delicacy (Singh & Bhatnagar, 2019). Furthermore, various parts of *M. longifolia* are utilized as cattle food and production of alcoholic beverages and soaps, while its flowers, containing fermentable sugars, are used as natural sweeteners in local culinary delights (Behera et al., 2011). *P. emblica* is renowned for its nutritious fruit and medicinal properties (Chatterjee and Sil, 2007). Additionally, ripe fruits of *T. bellirica* are commonly integrated with *Terminalia chebula* and *Phyllanthus emblica* in Ayurvedic preparations known as Triphala to treat eye conditions (Nadkarni, 1976).

Climate change poses a significant threat to India's forests, particularly the tropical dry and moist deciduous forests that encompass about 42% and 7.7% of the country's forest cover, respectively (Bahuguna et al., 2016). Rising greenhouse gas emissions and land use changes have led to temperature increases, altered precipitation patterns and more frequent extreme weather events, all of which are impacting forest ecosystems (Tubiello et al., 2013; Sinha, 2022; Roshani et al., 2022). Forests play a crucial role in regulating the Earth's climate by sequestering carbon, but they are also highly vulnerable to the impacts of climate change (Bhattacharya & Prasad, 2009; Bahuguna et al., 2016). In the past century, there was a documented temperature rise of 1.1 °C globally (IPCC, 2023) and it is anticipated that the global temperature may increase by a range of 3.3 to 5.7 °C by the end of the twenty-first century (Arias et al., 2021). The profound impact of climate change is the reduction in species diversity and the availability of suitable habitats (Jain et al., 2021). Tropical trees, functioning near their temperature tolerance limits, demonstrate greater sensitivity to temperature increases and possess a restricted ability to adjust to even minor temperature fluctuations anticipated in the future (Ryan, 2010). In humid tropical regions, trees are also negatively impacted by droughts, resulting in reduced survival (Machado et al., 2023). Our knowledge about the repercussion of climate change still remains limited, as many studies focus on national-level assessments of forests (Chaturvedi et al., 2011), with a notable scarcity of species-specific and regional-level investigations, primarily due to their considerable uncertainty (Arnell et al., 2019).

Forecasting and comprehending the effects of environmental changes on species composition and distribution under the past and future climatic scenarios is a crucial concern within the realms of biogeography and biological conservation (Ribeiro et al., 2019). Species distribution modelling (SDM) is a statistical technique that relates the geographic positions of a species to environmental variables, in order to predict its potential distribution under present, past and future climatic scenarios (Guisan & Zimmermann, 2000). The application of the SDM approach is growing in its usage within paleobiology that links neo and paleobiology, particularly in the fields of biogeography and macro-ecology (Svenning et al., 2011). SDM complements fossil pollen evidence by offering quantitative and possibly high-resolution past projection of the species distribution (Stigall & Lieberman, 2006). Also, it facilitates the formulation of statistically derived, testable ecological hypotheses concerning past distributions and communities, as well as their dynamics (Eckert, 2011; Richards et al., 2007). Utilizing SDMs to project past species distributions and complementing these projections with fossil pollen evidence serves as a valuable tool for validating the accuracy of such models (Nitin Saraf et al., 2024). MaxEnt is one of the prominent SDM software extensively employed for distribution modeling on a global scale (Phillips et al., 2006). MaxEnt is frequently preferred among these modeling approaches because it demonstrates superior performance when dealing with sparse data (Elith et al., 2006). These predictive capabilities have been involved in assessing potential habitats for ecologically and economically important tree species, from the tropical dry deciduous forest ecosystem. The expected high effect of changing climate on biodiversity is critical to know how climate change will impact species over an extended period of time. The unrecorded character of forest resources and their distribution poses a challenge in implementing relief measures for extensive forest damage. Therefore, it is essential to study how climate change affects key tree species of tropical dry deciduous forests.

In this study, we used MaxEnt software to construct species distribution models for five major NTFP species such as *Aegle marmelos*, *Buchanania lanzan*, *Madhuca longifolia*, *Phyllanthus emblica* and *Terminalia bellirica* in dry tropical forests of India. We assessed their potential distributions in the present, future and past climate scenarios. For past distribution, we complemented the mid-Holocene predicted distribution of the target species with the available fossil pollen evidence obtained from previous vegetation reconstruction studies. This integration holds significance in connecting paleoproxy research with species distribution modeling. Yadav et al. (2021) conducted a prior investigation assessing the potential distribution of key NTFP species in the Madhya Pradesh region that covered both current and projected future climatic scenarios under four RCPs (2050 and 2080). Notably, this study did not include an analysis of the past distribution of the target species and was exclusively focused on the Madhya Pradesh region. To address this gap, we formulated four main objectives for our study: (1) to identify the key environmental factors influencing species distribution, (2) to assess the current potential distribution, (3) to predict the impact of climate change in potential distributions of target species for the years 2050 and 2070 under RCP 2.6 and 8.5 and (4) to project potential distributions during mid-Holocene conditions. The results of this research contribute to a better understanding of the species' ecology and biology. Additionally, they offer valuable insights for future management and conservation practices, to mitigate the significant impact of global climate change.

Materials and methods

Target species

i. *Aegle marmelos*

A. marmelos, generally locally known as Bael in Hindi, is a medium-sized tree belonging to the Rutaceae family (Neeraj & Johar, 2017). It can be found in India but also in Egypt, Sri Lanka, Malaysia, Thailand, Bangladesh, Pakistan and Myanmar (Singh & Singh, 2021). It naturally grows in dry dipterocarp forests and mixed deciduous along with dry forest of southern and central India (Orwa et al., 2009). Although *A. marmelos* is considered a subtropical species, it exhibits a wide range of adaptation and can thrive in tropical, arid and semi-arid environments (Neeraj & Johar, 2017), in both dry environments and under high rainfall (Chundawat, 1990). It can thrive at an altitude of 1200 m and withstand temperatures ranging from 50 to − 7 °C without severe growth retardation. Bael prefers well-drained, slightly acidic to alkaline soils (pH 5–8), but can also grow in rocky, shallow and even alkaline soils (Patkar et al., 2012). It is an economically important tree species, valued for its ripe fruits, which have a delicious pulp used in jams, syrups and puddings. Bael also has numerous medicinal properties and is commonly used as an ingredient in Ayurvedic herbal remedies (Pathirana et al., 2020).

ii. *Buchanania lanzan*

B. lanzan, commonly known as Chironji in Hindi, holds significant socioeconomic importance and belongs to the family Anacardiaceae (Malik et al., 2012; Zeven & Wet, 1982). This tree is typically found in the wild within tropical deciduous forests of North, Western and Central India, especially in regions with monsoonal climates (Banerjee & Bandyopadhyay, 2015). It thrives at elevations up to 1200 m and prefers daytime temperatures between 32 and 42 °C, although it can tolerate a wider range of temperatures (5 to 48 °C). It requires an average annual rainfall of 1000–1500 mm, but can tolerate levels between 750 and 2200 mm. The tree grows well in rocky and gravelly red soils but cannot withstand waterlogged conditions. It prefers well-draining deep loam soil (Phogat et al., 2020). Chironji is valued for its medicinal properties, with every part of the tree used in Ayurvedic medicine to treat various conditions such as fever, colds, bowel disorders and rheumatism (Prasad, 2020).

iii. *Madhuca longifolia*

M. longifolia, locally known as Mahua in Hindi, is a medium to large deciduous tree characterized by its expansive crown belonging to the family Sapotaceae that grows in Nepal, India, Sri Lanka and Myanmar (Fern, 2014; Khare et al., 2018). It is also a prominent riparian tree (Sunil et al., 2010). Mahua thrives in dry tropical and subtropical forests at elevations between 1200 and 1800 m. It can withstand frost and temperatures between 2 and 46 °C, with annual rainfall between 550 and 1500 mm. It grows well in shallow rocky, clayey and calcareous soils but flourishes best in deep, sandy-loam soils with adequate drainage (Khare et al., 2018; Orwa et al., 2009). The tree serves multiple purposes, providing food, fodder and fuel (Patel et al., 2011). It is also recognized for its diverse medicinal benefits, particularly among indigenous communities in India, who utilized various parts of the plant to address ailments such as dental issues, rheumatism, cardiac ailments, ulcers and respiratory conditions like bronchitis (Awasthi et al., 1975).

iv. *Phyllanthus emblica*

P. emblica is a deciduous tree known as Aonla/Amla in Hindi or Indian gooseberry. According to ancient Indian legend, the Amla tree was the first tree to grow on Earth (Gantait et al., 2021). *P. emblica* is a subtropical species that can endure cold winters and hot summers (up to 46 °C) and grow at elevations up to 1800 m. It thrives in a wide range of well-drained soils, from sandy loam to clay with slightly acidic to alkaline pH (Orwa et al., 2009). The fruit of *P. emblica* is highly nutritious, containing vitamins, minerals and antioxidants. It is believed to enhance immunity against various illnesses and is widely utilized in Ayurveda (Bhagat, 2014).

v. *Terminalia bellirica*

T. bellirica is a large deciduous tree widespread across India, found up to 1000 m elevation (Kumar & Khurana, 2018). It grows best with mean annual temperatures of 22 to 28 °C, although it can survive temperatures ranging from 5 to 45 °C and prefers a mean annual rainfall of 900 to 3000 mm. It raises best in fertile, loam soils with adequate drainage; nevertheless, it has done quite well on poor soils (Orwa et al., 2009). The tree is valued for its wide range of pharmacological effects, including analgesic, antipyretic, anti-secretory, antimicrobial, antidiabetic, anti-diarrheal, antioxidant, anti-ulcer, anticancer and antidepressant-like activities. Its significant phytoconstituents, such as bellericanin, gallic acid and tannins, contribute to these effects (Kumar & Khurana, 2018).

Species occurrence records

The primary occurrence records for selected NTFP species were gathered through a field survey using the handheld Global Positioning System (GPS) Garmin from the forested regions of Maharashtra, Chhattisgarh, Madhya Pradesh and Uttar Pradesh. Secondary occurrence data points were extracted from open-source data repositories, i.e. iNaturalist (www.inaturalist.org accessed 22 May 2023), Indian Biodiversity Portal (indiabiodiversity.org/ procured 2 July 2023) and Global Biodiversity Information Facility (GBIF.org obtained 29 June 2023a, b, c, d, e). Since the entire target species are extensively distributed across India, it was not feasible to conduct thorough field visits across the entire India region for ground truthing. In order to encompass the widest possible range of species distribution, locations of species occurrences were supplemented with data from published literature and herbarium datasets maintained at the Botanical Survey of India in Allahabad and Dehradun; National Botanical Research Institute, Lucknow; Forest Research Institute, Dehradun; and Indian Virtual Herbarium (ivh.bsi.gov.in). Verification was conducted by superimposing the points into the Google Earth images to minimize potential errors resulting from coordinates obtained from secondary sources. In this study, exclusively geographic coordinates located within the borders of India, particularly within forested areas, were utilized. A total of 821 occurrence points for *A. marmelos*, 600 occurrence points for *M. longifolia*, 298 occurrence records for *B. lanzan*, 1001 occurrence records for *P. emblica* and 508 occurrence records for *T. bellirica* were obtained. Using the ArcGIS SDM toolkit in ArcGIS 10.5 software, redundant records were eliminated and spatially refined to ensure that each grid cell (1 km × 1 km) contained only one point. Finally, a total of 453, 320, 218, 577 and 314 occurrence points for *A. marmelos*, *M. longifolia*, *B. lanzan*, *P. emblica* and *T. bellirica*, respectively, were included into the model to predict their potential distribution.

Environmental variables

We obtained the current bioclimatic variables for evaluating the potential habitat suitability of the target species from the WorldClim database, version 1.4 (Hijmans et al., 2005). Furthermore, we incorporated three topographic variables such as elevation, aspect and slope. The probable future habitat suitability of target species was estimated for RCP 2.6 and 8.5 using the Hadley Global Environment Model 2-Earth System (HADGEM2-ES) reported by the Intergovernmental Panel for Climate Change (IPCC) in the fifth assessment report (AR5) (Moss et al., 2010). Additionally, past bioclimatic variables for the mid-Holocene (~ 6000 cal year BP) were derived using the WorldClim database. These variables were compiled from the simulations of General Circulation Models (Hijmans et al., 2005) built on HadGEM2-ES from the Coupled Model Intercomparison Project (CMIP) (Gent et al., 2011). All of the bioclimatic factors for present, future and past are at the finest spatial resolution of 30 arc s (1 km × 1 km) allowing for the development of a precise conservation plan.

Selection of environmental variables

The species distribution models focused on analyzing the collinearity among environmental variables and the occurrence points of the particular species. The input bioclimatic variables exhibit spatial autocorrelation; the true relationships may not emerge as different combinations of these variables can be used to project species distribution effectively. Correlations between bioclimatic variables lead to weak model and potentially false analyses (Dormann et al., 2013). Therefore, it is necessary to perform correlation tests, employing Pearson's correlation, to assess the associations between predictor variables. Highly associated bioclimatic parameters with correlation coefficients > 0.7 were removed from the final analysis (Yang et al., 2013) (Supplementary Table 1 a-e).

After the multi-collinearity test, out of 22 environmental variables, only 10 bioclimatic variables and 3 topographical variables were considered to model the distribution of the target species. The selected variables used to model the 5 targeted species have been listed in Table 1. They include the following: annual mean temperature (Bio_1), isothermality (Bio_3), mean diurnal range (Bio_2), mean temperature of wettest quarter (Bio_8) (except for *B. lanzan* and *T. bellirica*), mean temperature of driest quarter (Bio_9) (except for *P. emblica*), precipitation of driest month (Bio_14), annual precipitation (Bio_12), precipitation seasonality (Bio_15) (except for *B. lanzan*), precipitation of warmest quarter (Bio_18) (except for *A.

Table 1 Selected bioclimatic variables used for modelling the distribution of target species with their percentage contribution

Target species	*A. marmelos*	*B. lanzan*	*M. longifolia*	*P. emblica*	*T. bellirica*
Bioclimatic variables with percentage contribution	Bio_1 (11.6%)	Bio_1 (6.1%)	Bio_1 (13.3%)	Bio_1 (4%)	Bio_1 (15.4%)
	Bio_2 (1%)	Bio_2 (0.7%)	Bio_2 (7.2%)	Bio_2 (0.7%)	Bio_2 (0.5%)
	Bio_3 (4.1%)	Bio_3 (3.3%)	Bio_3 (6.3%)	Bio_3 (19.2%)	Bio_3 (4%)
	Bio_8 (0.4%)	Bio_9 (3.2%)	Bio_8 (0.3%)	Bio_8 (0.1%)	Bio_9 (0.3%)
	Bio_9 (0.2%)	Bio_12 (56.6%)	Bio_9 (1%)	Bio_12 (39.5%)	Bio_12 (52.3%)
	Bio_12 (39.7%)	Bio_14 (1.6%)	Bio_12 (43.4%)	Bio_14 (1.2%)	Bio_14 (1.1%)
	Bio_14 (5.3%)	Bio_18 (7.4%)	Bio_14 (1.4%)	Bio_15 (3.6%)	Bio_15 (5.8%)
	Bio_15 (2.8%)	Bio_19 (4.9%)	Bio_15 (4.4%)	Bio_18 (3.9%)	Bio_18 (4.6%)
	Bio_19 (12%)	Alt (8.5%)	Bio_18 (11.4%)	Bio_19 (16.1%)	Bio_19 (5.5%)
	Alt (9.5%)	Asp (1.3%)	Bio_19 (5%)	Alt (8.4%)	Alt (3.7%)
	Asp (1.2%)	Slope (6.2%)	Alt (9.5%)	Asp (0.9%)	Asp (0.9%)
	Slope (12.2%)		Asp (1.2%)	Slope (2.3%)	Slope (5.8%)
			Slope (12.2%)		

marmelos), precipitation of coldest quarter (Bio_19) and three topographic variables aspect, altitude and slope.

Model description

The study employed the maximum entropy (MaxEnt) species distribution modeling method (Phillips et al., 2006) to assess potential habitats for the chosen NTFP species across present, future and past climatic scenarios. Maximum Entropy Model performs remarkably well in comparison to other methods developed for estimating the species distributions, using presence-only data (Elith et al., 2006). The model was calibrated for the current climate and projected for past and future climatic scenarios. The projection for the past extended back to the mid-Holocene (~6000 cal year BP). Additionally, for future predictions, the model was utilized to forecast climatic conditions for the years 2050s and 2070s under RCP 2.6 and 8.5 scenarios. Randomly, 75% of the total occurrence data points were selected to train the model and the remaining 25% were used to test the model. The study employed 10 replications each with a maximum of 5000 iterations. We selected the jackknife test option to measure the variable contribution. A regularization multiplier of 1 was set as the default. Additionally, the following steps were implemented: (1) setting a random seed for every iteration and (2) maximum number of background points as 10,000. The remaining settings were set to default. The cloglog MaxEnt output was used to get a probability of species occurrence (Phillips et al., 2017).

Evaluation of the model

The MaxEnt model performance was measured by the Area Under the Curve (AUC) metric, which is commonly employed to evaluate Receiver Operating Characteristic (ROC) plots (Swets, 1988). The AUC values served as an indicator of the performance of model. AUC is calculated as the likelihood that an arbitrary presence will be categorized higher than a random background point (Merow et al., 2013). Yang et al. (2013) suggested that higher AUC scores indicate that the selected variables for prediction yield more accurate results, aligning closely with the provided training and test data. However, it is important to note that lesser AUC scores must not be considered a sign of poor model performance as the species with broader distributions tend to yield lesser AUC score (Yadav et al., 2021). The impact of every bioclimatic variable on the distribution of all NTFP species (*A. marmelos*, *B. lanzan*, *M. longifolia*, *P. emblica* and *T. bellirica)* was calculated using the jackknife procedure.

Compilation of fossil pollen data

We compiled fossil pollen records of target species during the mid-Holocene from previously published vegetation reconstruction studies (Supplementary

Table 2). To evaluate the efficiency of the SDM in projecting the past (mid-Holocene) distribution of target species, we complement the Middle Holocene projections with existing vegetation reconstruction studies based on the fossil pollen data. The integration involved overlaying fossil pollen data points on maps depicting mid-Holocene projections. This would serve to validate the past projections of target species through proxy-based evidence derived from fossil pollen data.

Calculation of area change

We utilized ArcGIS 10.5 software to compute the change in habitat suitability (%) for both future and past climatic scenarios for the target species. It calculates the complete area of suitable habitat across present, future and past scenarios in km^2 (Samal et al., 2023).

Results

Assessment of model performance

The AUC values range between 0 and 1. Values between 0.5 and 0.7 designate poor model performance, while those between 0.7 and 0.9 signify good model performance. AUC values exceeding 0.9 suggest outstanding model performance (Chakraborty et al., 2016; Swets, 1988). Based on Swets (1988) criteria, the precision of MaxEnt models for all target species, based on their AUC value (*A. marmelos*; AUC-0.728, *B. lanzan*; AUC-0.767, *M. longifolia*; AUC-0.753, *P. emblica*; AUC-0.724 and *T. bellirica*; AUC-0.770), indicated a good model performance (Supplementary Fig. 1a-e).

Jackknife test and response curves

In the MaxEnt model, the Jackknife test was conducted to identify variables of significant importance in predicting the potential distribution of species (Elith et al., 2011). The Jackknife test showed that, among the environmental factors considered in model creation, annual precipitation (Bio_12) followed by precipitation of the coldest quarter (Bio_19) and annual average temperature (Bio_1) were the most explanatory predictors demonstrating high regularized training gain had the greatest impact on the habitat suitability distribution for *A. marmelos*, *B. lanzan* and *T. bellirica*. Moreover, for *M. longifolia*, the Jackknife test indicated that annual precipitation (Bio_12) was the primary influential predictor, followed by annual mean temperature (Bio_1) and precipitation of the warmest quarter (Bio_18), with significant impact and high regularized training gain. In the case of *P. emblica*, the test revealed that annual precipitation (Bio_12) was the key important predictor, followed by isothermality (Bio_3) and precipitation during the coldest quarter (Bio_19) (Supplementary Fig. 2a-e).

The relationship between bioclimatic factors and potential species occurrence was indicated by the response curves. The response curves developed using the MaxEnt model depict the logistic predictions for all target species in response to variations in predictive variables, while keeping all additional environmental factors constant at average sample points. According to the response curve, the probability of a suitable habitat for *A. marmelos* remains high in regions where the annual precipitation (Bio_12) ranges between 900 and 3000 mm. Also, the precipitation of the coldest quarter (Bio_19) has a positive influence on its growth till 2000 mm, and then, it starts declining. The optimal conditions for the growth of *B. lanzan* include an annual rainfall range of up to 1200 mm, with elevation exerting a positive influence up to 1000 m; then, it starts to decline. The annual mean temperature (Bio_1) is significant for *M. longifolia*, with the most suitable range for this species falling between 20 and 24 °C. Additionally, annual precipitation (Bio_12) exerts a positive influence on *M. longifolia* between 1000 and 2000 mm. *P. emblica* experiences the most favourable growth conditions characterized by an annual rainfall range between 1000 and 2000 mm, with isothermality (Bio_3) exerting a positive influence from 30 to 36%. Lastly, *T. bellirica* responds positively to annual mean temperature for growth between 20 and 24 °C, and the most suitable environment for its growth encompasses an annual rainfall range between 1000 and 2000 mm. The response curves for all the targeted species have been shown in the Supplementary Fig. 3a-e. The blue bands in the response curves depict the standard deviation of each of the response curves.

Percentage contribution of environmental variables

Based on the percentage contribution, various environmental variables played a key role in driving the distribution patterns of the chosen NTFP species. For *A. marmelos*, annual precipitation (Bio_12) made the most substantial contribution, accounting to 39.7%, succeeded by precipitation of the coldest quarter (Bio_19) and annual mean temperature (Bio_1) with 12% and 11.6%, respectively. Altitude (Alt) and slope (Slope) were the dominant topographical factors, contributing 9.5% and 12.2%, respectively. For *B. lanzan*, annual precipitation (Bio_12) played a pivotal role, predicting 56.6% of its distribution. Annual mean temperature (Bio_1) and precipitation of the coldest quarter (Bio_19) were also significant factors, contributing 6.1% and 4.9%, respectively. Topographical variables, viz. altitude (Alt) and slope (Slope), also played major roles, contributing 8.5% and 6.2%, respectively. Furthermore, for *M. longifolia*, annual precipitation (Bio_12) emerged as the predominant factor, contributing to 43.4% of its distribution. Also, annual mean temperature (Bio_1), precipitation of the warmest quarter (Bio_18), mean diurnal range (Bio_2) and isothermality (Bio_3) also played substantial roles, contributing 13.3%, 11.4%, 7.2% and 6.3%, respectively. In case of *P. emblica*, annual precipitation (Bio_12) played a key role, contributed maximum with 39.7%. Isothermality (Bio_3), precipitation of the coldest quarter (Bio_19) and altitude (Alt) also held a significant role, contributing 19.2%, 16.1% and 8.4%, respectively. Finally, for *T. bellirica*, annual precipitation (Bio_12) emerged as the predominant factor, exerting a significant influence with 52.3% on its distribution. Annual mean temperature (Bio_1), precipitation of the coldest quarter (Bio_19), slope (Slope) and altitude (Alt) also played substantial roles, accounting for 15.4%, 5.5%, 5.8% and 3.7%, respectively (Table 1).

Potential present, future and past distribution of target species

i. *A. marmelos*

In the present climate scenario, the extremely suitable habitats of *A. marmelos* were predominantly located towards Siwalik hills, Western Ghats regions of Kerala and the Brahmaputra valley and Northeast hills in North-eastern India (depicted in red, 213,201.97 km^2) (Fig. 1a). Additionally, moderately to highly suitable habitats were found in the Upper and lower Gangetic plains, Chhota Nagpur plateau, Western Ghats, Gujarat Semi-arid region, South Deccan plateau, Eastern Ghats (orange, 774,584.59 km^2 and yellow, 1,001,072.35 km^2) (Fig. 1a; Table 2a). Under the RCP 2.6 (2050 and 2070), the model anticipated a decline in the suitable habitats for *A. marmelos* throughout India compared to the current distribution. Extremely suitable habitats would be estimated to decline in the Siwalik hills, Western Ghats of Kerala and Northeast hills and Brahmaputra valley in North-eastern India. Conversely, under the RCP 8.5 (2070), the model anticipates an expansion of extremely suitable habitats in the South Deccan plateau, Eastern plateau, East coast, Upper and lower Gangetic plains and Punjab plains (Fig. 1b–e). Under RCP 2.6, the area of extremely, highly and moderately suitable habitat is expected to decrease from its current range by 2.77%, 6.27% and 6.54% in 2050 and by 3.55%, 8.98% and 6.39% in 2070, respectively. Subsequently, in RCP 8.5, the area of extremely, highly and moderately suitable habitat is expected to decrease by 1.67%, 10.43% and 9.90% in 2050 and the extremely suitable habitat increased by 1.49%, while the highly and moderately suitable habitat is expected to decrease by 6.63% and 12.78% in 2070, respectively. During the mid-Holocene, the model indicated that extremely suitable habitats were present in the Punjab Plains, Upper Gangetic plains, Semi-arid Gujarat, Central Highlands, South Deccan plateau, Eastern plateau, Northeast hills and Brahmaputra valley. Most of the biogeographic zones of India (Gujarat Semi-arid regions, Deccan peninsula, Central Highlands, Eastern plateau) showed highly to moderately suitable habitats (Fig. 1f). Also, the mid-Holocene prediction showed a significant increase in extremely, highly and moderately suitable habitat by 3.11%, 8.06% and 8.52%, respectively (Table 3a). A map of India delineating biogeographic zones as classified by Rodgers et al. (2002) has been provided in Supplementary Fig. 4.

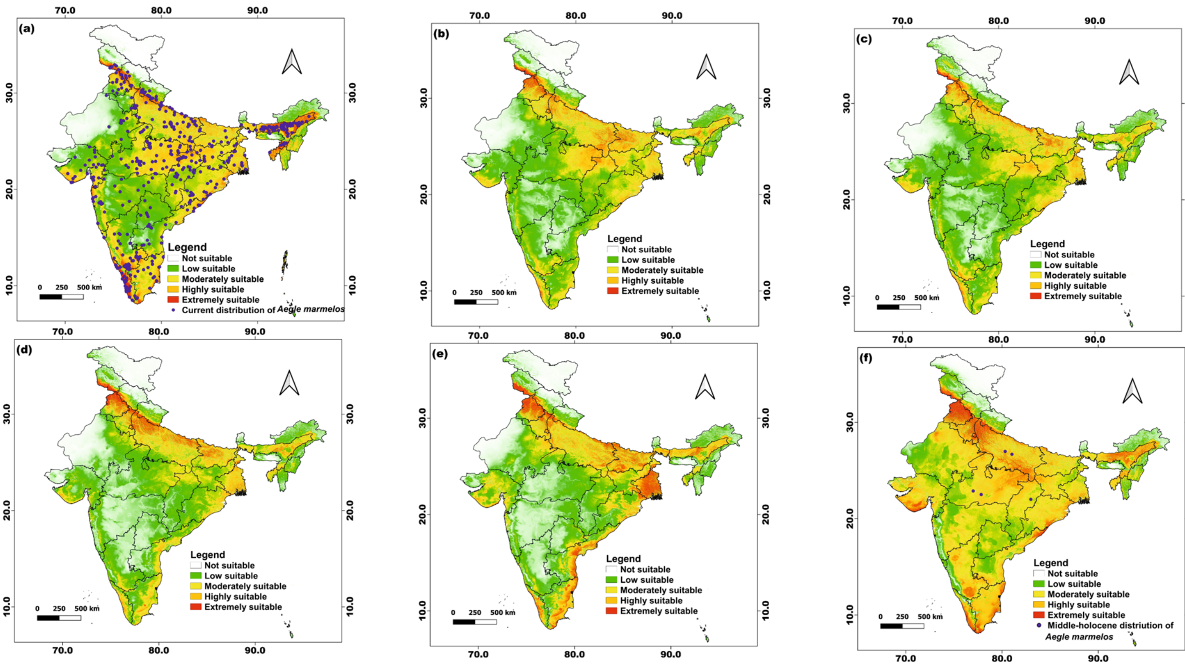

Fig. 1 **a** The current distribution of *A. marmelos* in India. **b** Predicted future distribution model of *A. marmelos* under RCP 2.6 (2050), **c** RCP 2.6 (2070), **d** RCP 8.5 (2050) and **e** RCP 8.5 (2070), **f** mid-Holocene distribution of *A. marmelos*

ii. *B. lanzan*

The extremely suitable habitats of *B. lanzan* under the current climatic scenario were primarily located in the Western Ghats, Central Highlands and Siwalik hills (red, 221,078.23 km^2). Furthermore, high to moderate suitable habitats were found in the Upper Gangetic plains, Central Highlands, Eastern plateau and Chhota Nagpur plateau (orange, 485,722.75 km^2 and yellow, 734,906.70 km^2). Karnataka, Telangana, Kerala, Andhra Pradesh, Tamil Nadu, Maharashtra, Bihar, West Bengal and the entire North-eastern India possessed low suitability for *B. lanzan* (green, 928,086.56 km^2) (Fig. 2a; Table 2b). Under the RCP 2.6 scenario (2050 and 2070), the model predicted an increase of extremely suitable habitats for *B. lanzan* in the Western Ghats regions, Upper Gangetic plains, Central Highlands, Eastern plateau and Chhota Nagpur plateau. In contrast, the RCP 8.5 scenario (2050 and 2070) predicted a decrease in the extremely suitable habitat within these regions, compared to the RCP 2.6 scenario (2050 and 2070) (Fig. 2b–e). In RCP 2.6, there is an increase in extremely and highly suitable habitat by 8.09% and 2.11% in 2050 and by 9.68% and 0.36% in 2070, respectively, while moderately and low suitable habitat is decreased by 0.41% and 2.94% in 2050 and 2.26% and 2.36% in 2070, respectively. Subsequently, in RCP 8.5, highly and moderately suitable habitat is expected to decrease by 0.42% and 5.72% in 2050 and by 3.07% and 6.35% in 2070, respectively. For the mid-Holocene, the model indicated that extremely suitable habitats were present in the Gujarat Semi-arid regions, Central Highlands, Central and South Deccan plateau, The majority of biogeographic zones in India, including Semi-arid regions of Gujarat and Rajasthan, entire Deccan peninsula, Upper Gangetic plains, Chhota Nagpur plateau and Eastern plateau exhibited highly and moderately suitable habitats (Fig. 2f). In the mid-Holocene, there was a significant increase in extremely suitable habitat by 5.46%, highly suitable habitat by 13.90% and moderately suitable habitat by 8.40% (Table 3b).

Table 2 Area in square kilometres (km^2) showing suitable habitats under past, current and future climatic scenarios for (a) *A. marmelos*, (b) *B. lanzan*, (c) *M. longifolia*, (d) *P. emblica* and (e) *T. bellirica*

Range	Habitat suitability	Current	Mid-Holocene	RCP 2.6 (2050)	RCP 2.6 (2070)	RCP 8.5 (2050)	RCP 8.5 (2070)
(a) *A. marmelos*							
0	Not suitable (white)	967,348.83 25.01%	557,793.63 14.42%	1,433,383.26 37.06%	1,477,654.32 38.20%	1,762,661.26 45.57%	1,772,858.27 45.84%
0–0.25	Low suitable (green)	911,505.60 23.57%	559,367.76 14.46%	1,048,308.51 27.10%	1,132,976.20 29.29%	966,816.06 25.00%	799,187.79 20.66%
0.25–0.50	Moderately suitable (yellow)	1,001,072.35 25.88%	1,330,652.53 34.40%	747,997.22 19.34%	753,881.87 19.49%	618,177.03 15.98%	506,809.47 13.10%
0.50–0.75	Highly suitable (orange)	774,584.59 20.03%	1,086,312.79 28.09%	531,987.28 13.75%	427,277.95 11.05%	371,301.75 9.60%	518,205.92 13.40%
0.75–1.00	Extremely suitable (red)	213,201.97 5.51%	333,589.44 8.62%	106,039.86 2.74%	75,923.00 1.96%	148,760.03 3.85%	270,651.89 7.00%
(b) *B. lanzan*							
0	Not suitable (white)	1,497,919.11 38.73%	754,102.23 19.50%	1,232,509.38 31.87%	1,288,195.49 33.31%	1,427,060.68 36.90%	1,453,378.41 37.58%
0–0.25	Low suitable (green)	928,086.56 24.00%	598,021.96 15.46%	814,562.81 21.06%	836,942.88 21.64%	102,5672.76 26.52%	1,259,772.71 32.57%
0.25–0.50	Moderately suitable (yellow)	734,906.70 19.00%	1,059,988.55 27.41%	719,230.42 18.60%	647,397.57 16.74%	513,640.65 13.28%	489,262.46 12.65%
0.50–0.75	Highly suitable (orange)	485,722.75 12.56%	1,023,461.71 26.46%	567,413.24 14.67%	499,602.66 12.92%	469,600.17 12.14%	367,077.71 9.49%
0.75–1.00	Extremely suitable (red)	221,078.23 5.72%	432,141.69 11.17%	534,000.28 13.81%	595,574.75 15.40%	431,741.88 11.16%	298,222.05 7.71%
(c) *M. longifolia*							
0	Not suitable (white)	1,309,910.75 33.87%	857,999.85 22.18%	1,580,988.49 40.88%	1,711,539.49 44.25%	2,485,733.58 64.27%	3,275,760.13 84.70%
0–0.25	Low suitable (green)	770,705.51 19.93%	557,747.14 14.42%	743,493.32 19.22%	738,477.09 19.09%	465,565.81 12.04%	226,670.93 5.86%
0.25–0.50	Moderately suitable (yellow)	949,679.09 24.55%	103,3691.27 26.73%	782,239.56 20.22%	737,216.30 19.06%	489,932.84 12.67%	192,352.34 4.97%
0.50–0.75	Highly suitable (orange)	620,297.89 16.04%	1,008,753.35 26.08%	513,874.95 13.29%	494,949.06 12.80%	352,137.83 9.10%	146,017.15 3.78%
0.75–1.00	Extremely suitable (red)	217,120.11 5.61%	409,524.53 10.59%	247,119.82 6.39%	185,531.40 4.80%	74,346.08 1.92%	26,912.80 0.70%
(d) *P. emblica*							
0	Not suitable (white)	846,632.23 21.89%	412,051.70 10.65%	947,855.77 24.51%	999,036.11 25.83%	1,250,935.05 32.34%	1,133,495.02 29.31%
0–0.25	Low suitable (green)	1,101,830.07 28.49%	254,550.70 6.58%	1,256,267.40 32.48%	1,360,400.26 35.17%	1,369,806.95 35.42%	1,526,811.44 39.48%
0.25–0.50	Moderately suitable (yellow)	1,165,076.30 30.12%	1,472,135.08 38.06%	1,059,878.83 27.40%	1,037,616.85 26.83%	916,219.64 23.69%	924,938.28 23.91%
0.50–0.75	Highly suitable (orange)	502,450.61 12.99%	1,261,848.93 32.63%	488,312.21 12.63%	359,908.10 9.31%	261,854.21 6.77%	240,903.23 6.23%
0.75–1.00	Extremely suitable (red)	251,724.14 6.51%	467,129.72 12.08%	115,401.92 2.98%	110,752.04 2.86%	68,900.29 1.78%	41,565.37 1.07%
(e) *T. bellirica*							
0	Not suitable (white)	138,9624.51 35.93%	582,220.16 15.05%	1,534,270.22 39.67%	1,619,430.69 41.87%	1,626,806.72 42.06%	1,236,950.99 31.98%

Table 2 (continued)

Range	Habitat suitability	Current	Mid-Holocene	RCP 2.6 (2050)	RCP 2.6 (2070)	RCP 8.5 (2050)	RCP 8.5 (2070)
0–0.25	Low suitable (green)	929,177.20 24.02%	415,350.60 10.74%	1,104,626.88 28.56%	1,111,048.94 28.73%	1,013,165.21 26.20%	814,595.35 21.06%
0.25–0.50	Moderately suitable (yellow)	782,829.05 20.24%	1,062,170.77 27.46%	661,770.28 17.11%	610,604.82 15.79%	500,136.36 12.93%	531,925.91 13.75%
0.50–0.75	Highly suitable (orange)	518,856.77 13.42%	1,113,595.64 28.79%	481,533.11 12.45%	444,914.23 11.50%	568,184.04 14.69%	1,009,193.14 26.09%
0.75–1.00	Extremely suitable (red)	247,225.81 6.39%	694,378.97 17.95%	85,515.66 2.21%	81,714.67 2.11%	159,423.80 4.12%	275,047.94 7.11%

Table 3 Percentage change in suitable habitat area for (a) *A. marmelos*, (b) *B. lanzan*, (c) *M. longifolia*, (d) *P. emblica* and (e) *T. bellirica*

Range	Habitat suitability	Current-MH (%)	Current-RCP 2.6, 2050 (%)	Current-RCP 2.6, 2070 (%)	Current-RCP 8.5, 2050 (%)	Current-RCP 8.5, 2070 (%)
(a) *A. marmelos*						
0	Not suitable (White)	−10.59	12.05	13.19	20.56	20.83
0–0.25	Low suitable (Green)	−9.10	3.54	5.73	1.43	−2.90
0.25–0.50	Moderately suitable (Yellow)	8.52	−6.54	−6.39	−9.90	−12.78
0.50–0.75	Highly suitable (Orange)	8.06	−6.27	−8.98	−10.43	−6.63
0.75–1	Extremely suitable (Red)	3.11	−2.77	−3.55	−1.67	1.49
(b) *B. lanzan*						
0	Not suitable (White)	−19.23	−6.86	−5.42	−1.83	−1.15
0–0.25	Low suitable (Green)	−8.53	−2.94	−2.36	2.52	8.58
0.25–0.50	Moderately suitable (Yellow)	8.40	−0.41	−2.26	−5.72	−6.35
0.50–0.75	Highly suitable (Orange)	13.90	2.11	0.36	−0.42	−3.07
0.75–1	Extremely suitable (Red)	5.46	8.09	9.68	5.45	1.99
(c) *M. longifolia*						
0	Not suitable (White)	−11.68	7.01	10.38	30.40	50.83
0–0.25	Low suitable (Green)	−5.51	−0.70	−0.83	−7.89	−14.07
0.25–0.50	Moderately suitable (Yellow)	2.17	−4.33	−5.49	−11.89	−19.58
0.50–0.75	Highly suitable (Orange)	10.04	−2.75	−3.24	−6.93	−12.26
0.75–1	Extremely suitable (Red)	4.97	0.78	−0.82	−3.69	−4.92
(d) *P. emblica*						
0	Not suitable (White)	−11.24	2.62	3.94	10.45	7.42
0–0.25	Low suitable (Green)	−21.91	3.99	6.69	6.93	10.99
0.25–0.50	Moderately suitable (Yellow)	7.94	−2.72	−3.30	−6.43	−6.21
0.50–0.75	Highly suitable (Orange)	19.63	−0.37	−3.69	−6.22	−6.76
0.75–1	Extremely suitable (Red)	5.57	−3.52	−3.64	−4.73	−5.43
(e) *T. bellirica*						
0	Not suitable (White)	−20.88	3.74	5.94	6.13	−3.95
0–0.25	Low suitable (Green)	−13.29	4.54	4.70	2.17	−2.96
0.25–0.50	Moderately suitable (Yellow)	7.22	−3.13	−4.45	−7.31	−6.49
0.50–0.75	Highly suitable (Orange)	15.38	−0.97	−1.91	1.28	12.68
0.75–1	Extremely suitable (Red)	11.56	−4.18	−4.28	−2.27	0.72

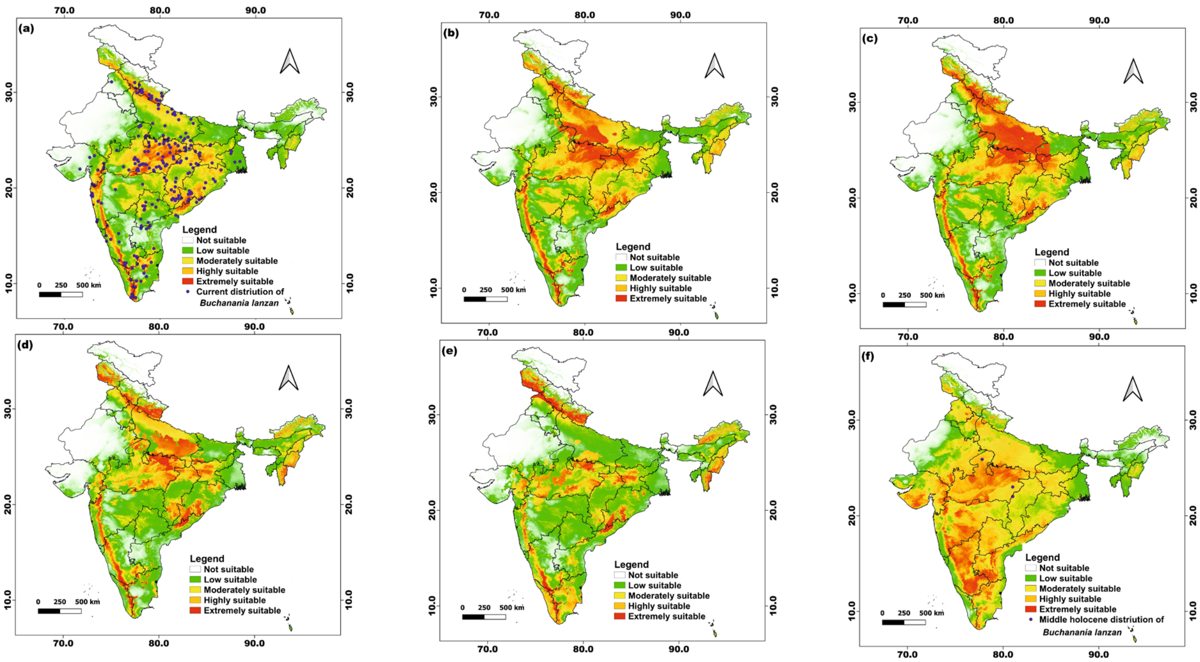

Fig. 2 **a** The current distribution of *B. lanzan* in India. **b** Predicted future distribution model of *B. lanzan* under RCP 2.6 (2050), **c** RCP 2.6 (2070), **d** RCP 8.5 (2050) and **e** RCP 8.5 (2070) f mid-Holocene distribution of *B. lanzan*

iii. *M. longifolia*

The extremely suitable habitats for *M. longifolia* were primarily concentrated in the Western Ghats regions, Central Highlands and South Deccan Peninsula in the current climatic scenario (red, 217,120.11 km^2). Additionally, Western Ghats Malabar Plains, Eastern plateau, Chhota Nagpur plateau and Gangetic plains exhibited highly and moderately suitable habitats (orange, 620,297.89 km^2 and yellow, 949,679.09 km^2) (Fig. 3a; Table 2c). Under the RCP 2.6 (2050 and 2070), extremely suitable habitats would be projected to be retained in the Western Ghats regions. Interestingly, there would be an increase in these habitats in the regions of Central Highlands and Upper Gangetic plains. Alternatively, under the RCP 8.5 (2050 and 2070), the model forecasts a significant decline in the extremely suitable habitats in the Western Ghats regions, Central Highlands and the Siwalik hills (Fig. 3b–e). Under RCP 2.6, the highly, moderately and low suitable habitat is expected to decrease from its current range by 2.75%, 4.33% and 0.70% in 2050 and by 3.24%, 5.49% and 0.83% in 2070, respectively. Under RCP 8.5, the extremely, highly, moderately and low suitable habitat is expected to decrease from its current range by 3.69%, 6.93%, 11.89% and 7.89% in 2050 and by 4.92%, 12.16%, 19.58% and 14.07% in 2070, respectively. Furthermore, during the mid-Holocene, the model indicated extremely suitable habitats in the Western Ghats, Semi-arid region of Gujarat and Rajasthan, Central Highlands and Upper Gangetic plains. Most of the biogeographic zones in India, including the complete Deccan peninsula, Upper Gangetic plains, Chhota Nagpur plateau and Eastern plateau, showed highly and moderately suitable habitats (Fig. 3f). Furthermore, our result revealed that, during mid-Holocene, there is a significant increase in extremely suitable habitat by 4.97%, highly suitable habitat by 10.04% and moderately suitable habitat by 2.17% (Table 3c).

iv. *P. emblica*

In the present climate condition, the extremely suitable habitats of *P. emblica* were primarily located in Siwalik hills, Western Ghats, Assam hills and Brahmaputra valley in North-eastern India (red, 251,724.14 km^2). Furthermore, Central Highlands,

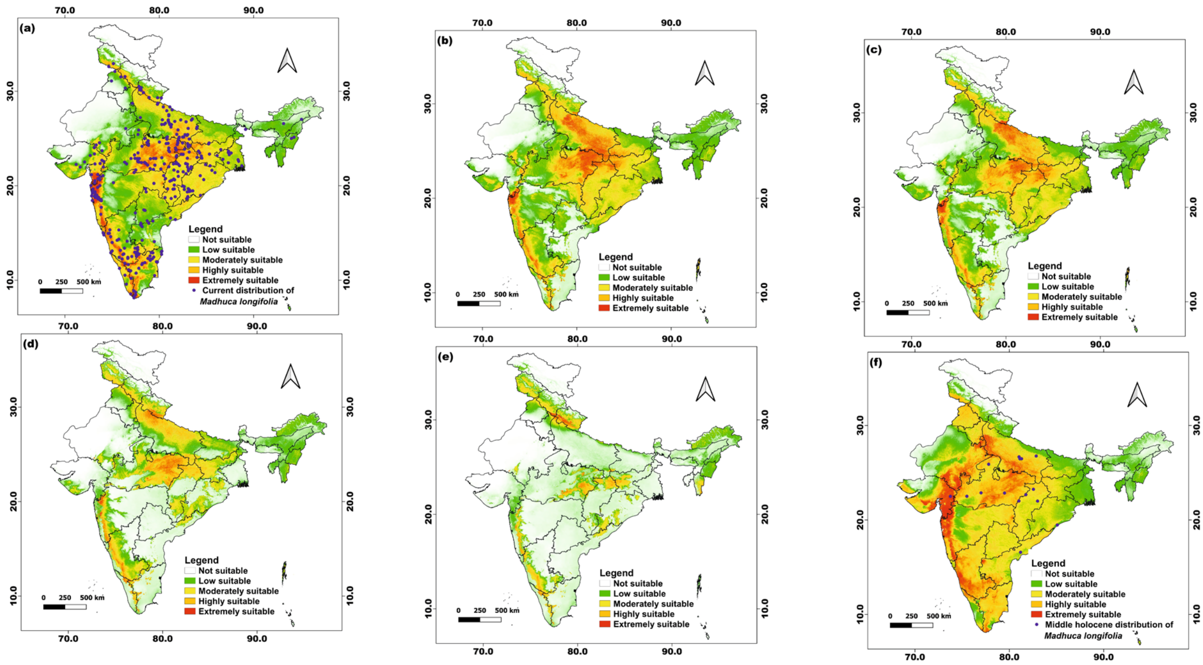

Fig. 3 **a** The current distribution of *M. longifolia* in India. **b** Predicted future distribution model of *M. longifolia* under RCP 2.6 (2050), **c** RCP 2.6 (2070), **d** RCP 8.5 (2050) and **e** RCP 8.5 (2070) **f** mid-Holocene distribution of *M. longifolia*

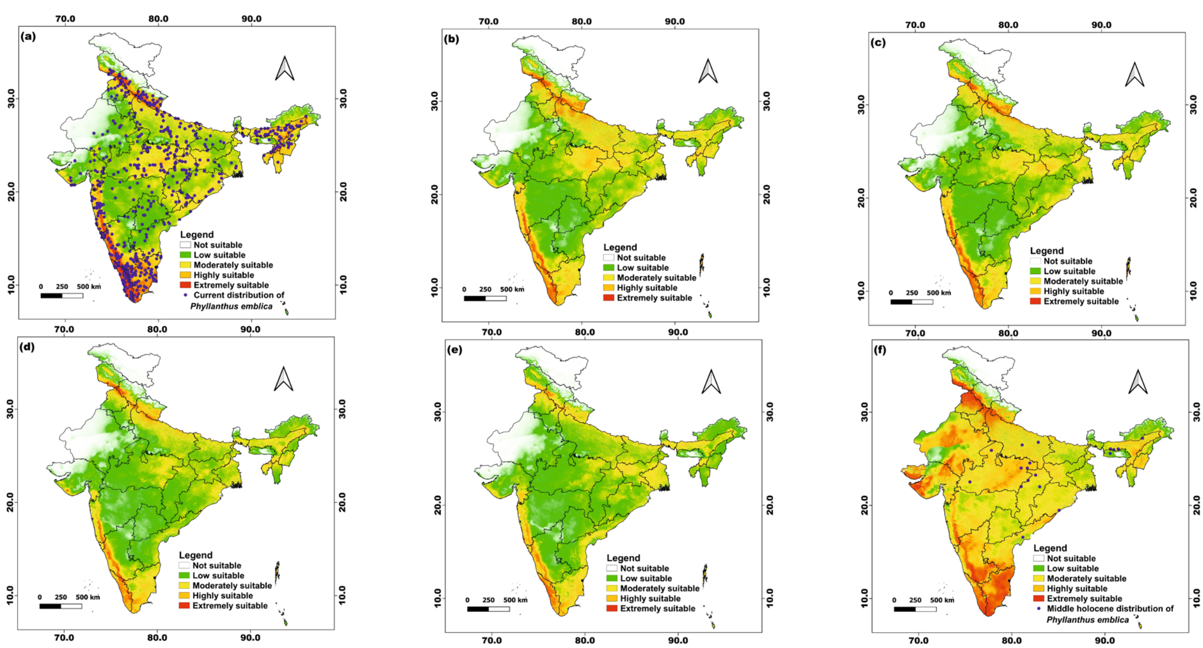

Fig. 4 **a** The current distribution of *P. emblica* in India. **b** Predicted future distribution model of *P. emblica* under RCP 2.6 (2050), **c** RCP 2.6 (2070), **d** RCP 8.5 (2050) and **e** RCP 8.5 (2070) **f** mid-Holocene distribution of *P. emblica*

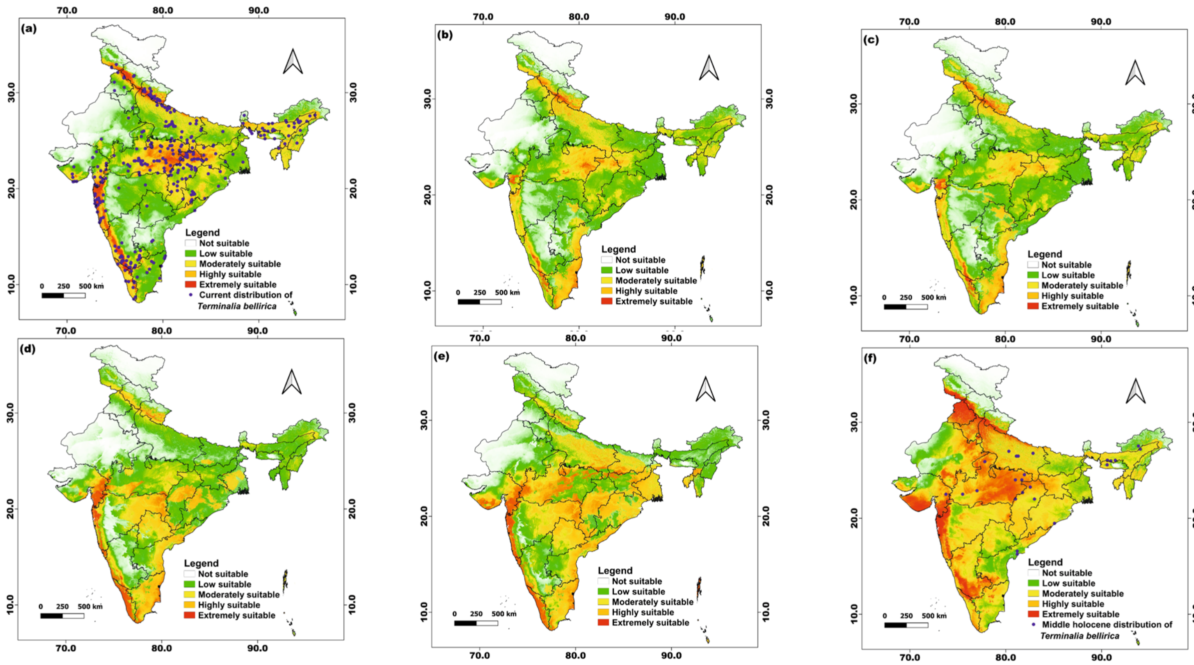

Fig. 5 **a** The current distribution of *T. bellirica* in India. **b** Predicted future distribution model of *T. bellirica* under RCP 2.6 (2050), **c** RCP 2.6 (2070), **d** RCP 8.5(2050) and **e** RCP 8.5 (2070) **f** mid-Holocene distribution of *T. bellirica*

South Deccan Plateau, Eastern plateau, Chhota Nagpur plateau and North-East hills exhibited highly and moderately suitable habitats (orange, 502,450.61 km^2 and yellow, 1,165,076.30 km^2) (Fig. 4a; Table 2d). Under the RCP 2.6 and 8.5 (2050 and 2070), there would be a decline in conducive habitats compared to the current distribution. Extremely suitable habitats would be expected to decrease in the Siwalik hills, Western Ghats, Central Highlands, Assam hills and Brahmaputra valley in North-eastern India (Fig. 4b–e). Under RCP 2.6, the area of extremely, highly and moderately suitable habitat is projected to decrease by 3.52%, 0.37% and 2.72% in 2050 and by 3.64%, 3.69% and 3.30% in 2070, respectively. RCP 8.5 is a high-emission climate change scenario, where the loss of suitable habitat is projected to be more severe, with a decrease of extremely, highly and moderately suitable habitat by 4.73%, 6.22% and 6.43% in 2050 and by 5.43%, 6.76% and 6.21% in 2070, respectively. During the mid-Holocene, the model indicated the extremely suitable habitats in the Gir range in Gujarat, the Western Ghats regions (Kerala and Karnataka), the complete Tamil Nadu and the Punjab and Delhi regions. Only a few states in India had low suitable habitats such as Himachal Pradesh, Mizoram, Jammu and Kashmir, Arunachal Pradesh, Manipur and Nagaland in North-eastern India and the remaining states have highly or moderately suitable habitats (Fig. 4f). In mid-Holocene, there was a significant increase in extremely, highly and moderately suitable habitats by 5.57%, 19.63% and 7.94% for *P. emblica* (Table 3d).

v. *T. bellirica*

The extremely suitable habitats of *T. bellirica* were mainly distributed in the Western Ghats, Central Highlands and Siwalik hills under the current climatic scenario (red, 247,225.81 km^2). Additionally, Western Ghats regions, Central Highlands, Chhota Nagpur plateau, Eastern plateau and North-eastern India were characterized by highly and moderately suitable habitats (orange, 518,856.77 km^2 and yellow, 782,829.05 km^2) (Fig. 5a; Table 2e). Under the RCP 2.6 scenario (2050 and 2070), there would be a projected decrease in extremely suitable habitats in the Western Ghats, Central Highlands, North-East hills and Siwalik hills. However, under the RCP 8.5 scenario (2070), there would be a notable increase in extremely suitable habitat, particularly in the Western Ghats, Central

Highlands, South Deccan plateau, Eastern plateau and East coast for *T. bellirica* (Fig. 5b–e). Under RCP 2.6, the area of extremely, highly and moderately suitable habitat is projected to decrease by 4.18%, 0.97% and 3.13% in 2050 and by 4.28%, 1.91% and 4.45% in 2070, respectively. Furthermore, our results showed, under RCP 8.5 (2070), an increase in extremely and highly suitable habitat compared to the current range by 0.72% and 12.68% and a decrease in moderately, low and unsuitable suitable habitat by 6.49%, 2.96% and 3.95%, respectively, in the year 2070. Moreover, during the mid-Holocene, the model revealed extremely suitable habitats in the Punjab Plains, Western Ghats, Upper Gangetic plains, Central Highlands and Gujarat Semi-arid regions. Entire Deccan peninsula, Eastern plateau, Chhota Nagpur plateau, Semi-arid regions of Gujarat and Rajasthan and North-eastern India demonstrated highly and moderately suitable habitats (Fig. 5f). During the mid-Holocene, there was a significant increase in extremely suitable habitat by 11.56%, highly suitable habitat by 15.38% and moderately suitable habitat by 7.22% (Table 3e).

Mid-Holocene pollen records of target species

Two fossil pollen records of *A. marmelos* were obtained from Uttar Pradesh, positioned within the range of extremely suitable habitat. Furthermore, two fossil pollen records were collected from Madhya Pradesh and one from Chhattisgarh, both situated in moderately suitable in the mid-Holocene projections (Fig. 1f). As for *B. lanzan*, a total of three fossil pollen records were compiled from Madhya Pradesh, positioned within the past projections of highly and moderately suitable habitats (Fig. 2f). In the case of *M. longifolia*, a total of 15 fossil pollen records were assembled from various regions in India. Four of these records were collected from Madhya Pradesh, situated within the range of extremely and highly suitable habitats. Additionally, six records were gathered from Uttar Pradesh, situated within highly suitable habitats and four from Chhattisgarh, located within moderately suitable habitats. One fossil record each was acquired from Gujarat and Andhra Pradesh located in extremely and low suitable habitats, respectively in the mid-Holocene projections (Fig. 3f). A total of 18 fossil pollen records were gathered for *P. emblica* from diverse regions in India. Among these, five were gathered from Madhya Pradesh, situated within the range of high to moderate suitability. Also, two records were compiled from Uttar Pradesh and four in Chhattisgarh, both positioned within moderately suitable habitats. One record each was acquired from Andhra Pradesh and Odisha, situated in low and moderately suitable habitats, respectively. Furthermore, three records were collected from Assam and two from Meghalaya, both found within moderately and low suitable habitats, respectively (Fig. 4f). A total of 26 fossil pollen records were compiled for *T. bellirica* from diverse regions in India. Among these, six were identified in Madhya Pradesh, situated within extremely suitable habitats. Moreover, four records were gathered from Uttar Pradesh, covered areas with high to moderate suitability and an additional four from Chhattisgarh, fallen within the moderately to low suitable habitats. Two records were retrieved from Andhra Pradesh and one from Odisha, located in low and moderately suitable habitats, respectively. Furthermore, a single fossil record was collected from Gujarat, positioned in an extremely suitable habitat. Additionally, three records were obtained from both Assam and Meghalaya and one record from Arunachal Pradesh, all situated within habitats categorized as moderately and low suitable, respectively in the mid-Holocene projections (Fig. 5f). Detail information about the fossil pollen locality has been provided in Supplementary Table 2.

Discussion

Climate change impact on target species

The current study revealed that the future climatic change would lead to an increase in the suitable habitat for *A. marmelos* and *T. bellirica*, while, conversely for *B. lanzan*, *M. longifolia* and *P. emblica*, the suitable habitat would decrease in RCP 8.5 (2050 and 2070). The extremely suitable habitat of *A. marmelos* would be increased and potentially shift to the South Deccan plateau, Eastern plateau, East coast, Upper and lower Gangetic plains and Punjab plains, under RCP 8.5 in 2070. Specifically, the Central Northeast region (including Uttar Pradesh, Bihar and West Bengal) is expected to undergo a considerable 19% (16 to 22%) increase in summer monsoon precipitation. Likewise, the peninsular region (encompassing

Eastern Ghats) is forecasted to witness a 4.7% increase in precipitation on average (1 to 9%) (Patwardhan et al., 2018). This shift could be attributed to the anticipated increases in monsoon precipitation, which would likely create more favourable conditions for the species in these areas. Additionally, these regions characterized by moderate to high altitudes, featuring an optimal amalgamation of precipitation and temperature, were found to be conducive for the growth of *A. marmelos* (Waheed et al., 2023). *A. marmelos* exhibits a broad spectrum of adaptability, allowing it to flourish in tropical, arid and semi-arid climates, displaying resilience in both arid and high rainfall conditions (Chundawat, 1990; Neeraj & Johar, 2017). It demonstrates remarkable drought resistance, thriving at high altitudes up to 1200 m and sustaining growth without hindrance at temperatures from − 7 to 50 °C and mean annual rainfall between 570 and 2000 mm (Pathirana et al., 2020). The ecological adaptability of *A. marmelos*, including its drought resistance, tolerance to diverse soils and resilience in both arid and high rainfall conditions, contributes to its projected increase in extremely suitable habitat under the RCP 8.5 scenario. For *T. bellirica*, under the RCP 8.5 scenario (2070), there would be a notable increase in extremely suitable habitat, particularly in the Western Ghats, Central Highlands, South Deccan plateau, Eastern plateau and East coast. This could be linked to the expected rise in monsoon rainfall, which is likely to establish more favourable environments for the species in these regions. Specifically, the West Central area (encompassing the Western Ghats and Madhya Pradesh) is anticipated to experience a substantial 16.7% increase in summer monsoon precipitation, ranging from 15 to 20%. Similarly, the peninsular region (including the Eastern Ghats) is forecasted to see a 4.7% increase in precipitation, on average ranging from 1 to 9% (Patwardhan et al., 2018). Therefore, the *T. bellirica*'s capacity to withstand the wide range of temperatures and precipitation variations, coupled with its notable resilience to drought and frost, as well as its ability for thriving in on poor and dry soils across a diverse pH range, are anticipated to lead to an expansion of its extremely suitable habitat in the RCP 8.5.

Deviations in precipitation and temperature can significantly impact the metabolic and phenological activities of species (Waheed et al., 2023). The effect of climate change on the phenology of tropical species is uncertain due to their diverse physiological adaptability to temperature shifts (Kailash et al., 2022). The suitable habitat of *A. marmelos* and *Terminalia bellirica* is influenced by a complex interaction between rising temperatures, changes in precipitation patterns and the species' ecological characteristics. Both species are expected to exhibit resilience to future climate changes and are projected to be minimally affected.

Conversely, the suitable habitat for *M. longifolia*, *B. lanzan* and *P. emblica* would be decreased under RCP 8.5 (2050 and 2070). Under RCP 8.5, the global surface temperatures are projected to rise by 3.3 to 5.7 °C over the years 2081–2100 (Arias et al., 2021; Kumar et al., 2006). Moreover, as the global mean temperature rises by the end of the twenty-first century, there is an anticipated increase in both the intensity and frequency of precipitation in India (Bhowmick et al., 2019; Kumar et al., 2006; Mishra et al., 2020). This will directly impact the suitability of habitats for *M. longifolia*, which is adapted to specific temperature (2 to 46 °C) and precipitation range (550–1500 mm) (Orwa et al., 2009). Higher temperatures may exceed the species' thermal tolerance, rendering previously suitable habitats less suitable, while deviations from specific rainfall regimes can also affect its ability to thrive, with extended drought periods or excessive rainfall potentially stressing the species (Sinha, 2022). *M. longifolia* thrives optimally in soils with deep loamy or sandy-loam composition that allow for proper drainage (Khare et al., 2018). Variations in precipitation patterns, coupled with increased temperatures, can influence soil moisture levels. Overall, the suitable habitat of *M. longifolia* is experiencing a gradual decline due to the anticipated alterations in temperature, precipitation patterns, soil conditions and extremely poor regeneration capacity (Garai et al., 2021).

Our results align with Garai et al. (2021) and Yadav et al. (2021), which indicate that the suitable habitat for *M. longifolia* is expected to decrease under future climatic change scenarios due to projected changes in climate conditions. Furthermore, *B. lanzan* has specific temperature requirements (32 to 42 °C) and precipitation ranges (1000–1500 mm) for its optimal growth and reproduction (Orwa et al., 2009). Under the RCP 8.5 scenario, it is anticipated that there will be significant rises in global temperatures and shifts in precipitation patterns (Arias et al., 2021; Bhowmick et al., 2019). These alterations can have a direct or indirect influence on the distribution of species (Priti et al., 2016). In summary, a decrease in extremely suitable habitats for *B. lanzan* in the specified regions can be attributed to a combination of the species' poor regeneration capacity and physical requirements (temperature, precipitation and soil conditions) and the projected changes in climate conditions in RCP 8.5 scenario (Mishra et al., 2021a).

Lastly, the *P. emblica* is a subtropical rather than strictly tropical species. It is sensitive to high temperatures. For optimum growth and development, it requires a narrow range of rainfall, i.e. 630–800 mm (Wali et al., 2015). High rainfall or irregular patterns can lead to water stress, impacting their growth and distribution. Due to intolerance to excessive heat and specific range of annual rainfall, the suitable habitat of *P. emblica* would be decreased under future climatic change scenarios. The RCP 8.5 scenario is expected to bring about substantial increases in global temperatures and alterations in precipitation patterns (Arias et al., 2021; Bhowmick et al., 2019). Our findings align with the conclusions presented by Yadav et al. (2021), suggesting an expected reduction in the favourable habitat for *P. emblica* for all RCPs for the years 2050 and 2080 due to anticipated climate changes.

Extremely high-temperature conditions with rainfall seasonality in the future would have a negative impact on the growth and reproduction of B. *lanzan*, *M. longifolia* and *P. emblica*. These species are highly sensitive to high temperatures and alterations in rainfall patterns. Various factors, including habitat disruption, climate change, pollution, overexploitation and invasive species, are recognized as significant threats to both plant species and overall global biodiversity (Hirsch, 2010). These variables have been shown to impact growth and reproductive processes, changing the phenological patterns of trees and also affecting the species distribution on a regional level (Sinha, 2022; Thakur et al., 2022). The reduction in habitat suitability for *B. lanzan*, *M. longifolia* and *P. emblica* in future climate scenarios is primarily due to the increase in temperature and shifts in rainfall patterns across India (Garai et al., 2021; Mishra et al., 2021a). Hence, an increase in the suitable habitat for *A. marmelos* and *T. bellirica* and a significant reduction of *B. lanzan*, *M. longifolia* and *P. emblica* for future climatic conditions confirm the impact of climate change on the target species. Our findings are consistent with the earlier research carried out by various researchers who reported climate change's impact on key plant species of tropical deciduous forest. Mishra et al. (2021b) identified a shift in the conducive habitat of *Shorea robusta* due to climate change. Tiwari et al. (2021) anticipated approximately 9–13% decline in the habitat suitability of *Butea monosperma* by 2050. Furthermore, Yadav et al. (2021) examined the influence of climate change on the distribution of five significant (NTFP) species, such as *Buchanania lanzan*, *Terminalia chebula*, *Emblica officinalis*, *Madhuca longifolia*, *Terminalia bellirica* and *Sterculia urens* in Central India. Their findings indicated a decrease in highly suitable for all five species except *Madhuca longifolia* under projected future climate scenarios. Deb et al. (2017) projected a diminishing habitat range for tropical deciduous tree species, including *Dipterocarpus turbinatus* and *Shorea robusta.* Ray et al. (2016) concluded that climate has a substantial role in shaping the distribution patterns of rubber tree, *Hevea brasiliensis*. Their research indicates that the North-eastern region would become more conducive for rubber tree cultivation, while further expansion in the Western Ghats region may be restricted by the projected climate conditions for 2050. Kailash et al. (2022) reported that *T. chebula* exhibits a high vulnerability to the climate change impacts and its distribution is likely to decrease across all RCPs for the year 2070. Another study by Mishra et al. (2021a) suggested the suitable habitat and population of *Buchanania cochinchinensis* undergo alterations due to climate changes.

Validation of past projections (mid-Holocene) of target species with fossil pollen records

Fossil pollen records were compiled across various Indian states for the target species. In the mid-Holocene projections, fossil pollen records of *A. marmelos* were situated within the range of extremely and moderately suitable habitats, supporting the distribution of species in Uttar Pradesh, Madhya Pradesh and Chhattisgarh (Fig. 1f). For *B. lanzan*, the fossil pollen records were found within the range of highly and moderately suitable habitats in mid-Holocene projections, providing substantial evidence for the species' presence and distribution in Madhya Pradesh (Fig. 2f). Furthermore, *M. longifolia*'s fossil pollen records were identified within the range of extremely to moderately suitable habitats in mid-Holocene projections. This robustly supports the suitability of *M. longifolia* in Gujarat, Madhya Pradesh, Odisha, Chhattisgarh, Uttar Pradesh and Andhra Pradesh, as supported by the fossil pollen records (Fig. 3f). For *P. emblica*, the fossil pollen records were situated within the range of high to moderate suitability in mid-Holocene projections. These findings strongly support the suitability of *P. emblica* in Uttar Pradesh, Madhya Pradesh, Chhattisgarh, Andhra Pradesh, Odisha, Assam and Meghalaya, as evidenced by the fossil pollen records (Fig. 4f). *T. bellirica* fossil pollen records were positioned within the range of high to moderate to low suitable habitats. These records robustly support the distribution of *T. bellirica* in Uttar Pradesh, Madhya Pradesh, Andhra Pradesh, Chhattisgarh, Odisha, Assam, Meghalaya and Arunachal Pradesh (Fig. 5f).

Future priority conservation zones in India

Species distribution modelling serves as a valuable tool in designing efficient conservation policies by producing predictive maps depicting the spatial extent of a species within a specified region (Hamid et al., 2019). Based on MaxEnt modelling, the distribution pattern of five major NTFP species, such as *A. marmelos*, *B. lanzan*, *M. longifolia*, *P. emblica* and *T. bellirica* is predicted under climate change scenarios. It has been suggested that NTFPs should be harvested with limited influence on the forest ecosystem (Marshall et al., 2003). The growing market demand for various NTFPs in current times has caused an increased extraction rate from the forest, with much of the research predominantly focusing on the socioeconomic aspects of these products (Silori et al., 2005). Our study revealed an increase in the extremely suitable habitat for *A. marmelos* and *T. bellirica*; however for *B. lanzan*, *M. longifolia* and *P. emblica*, it would be decreased under RCP 8.5. Therefore, the results of this study hold potential for formulating a conservation and management framework for these NTFP species in India. This involves identifying critical conservation areas and identifying regions that are likely to be climatically suitable for implementing restoration strategies. Primarily, for *A. marmelos*, emphasis should be placed on implementing restoration strategies in the South Deccan plateau, Eastern plateau, East coast, Upper and lower Gangetic plains and Punjab plains, and for *T. bellirica*, efforts should be concentrated on the Western Ghats, Central Highlands, South Deccan plateau, Eastern plateau and East coast. These areas are projected to see an expansion of extremely suitable habitats for these species under future climatic conditions, hence to promote the growth of these species. Secondly, for *B. lanzan*, conservation efforts should be concentrated in the Western Ghats regions, Upper Gangetic plains, Central Highlands, Eastern plateau and Chhota Nagpur plateau. For *M. longifolia*, priority areas include the Western Ghats regions, Central Highlands and the Siwalik hills. Finally, for *P. emblica*, emphasis should be placed on the Siwalik hills, Western Ghats, Central Highlands, Assam hills and Brahmaputra valley in North-eastern India, where suitability is anticipated to be sustained in future climatic conditions (RCP 8.5 in 2070). Hence, we advocate for proactive restoration and conservation measures for the habitats of target species that currently exist and are anticipated to persist in future climatic scenarios. Preservation and re-establishment policies for major NTFP species must be designed and implemented in consultation with native peoples, taking into account their expectations and aspirations.

Study limitations

This study highlights the effectiveness of species distribution modeling methods in projecting the suitable habitat of key NTFP species in India—such as *A. marmelos*, *B. lanzan*, *M. longifolia*, *P. emblica* and *T. bellirica* in India. The utilization of the MaxEnt model in this study represents a robust method for predicting species distribution. As the primary aim of this study was to evaluate species susceptibility to climate change, solely bioclimatic variables were used in the model. While the MaxEnt modeling approach demonstrated effectiveness in previous surveys with the bioclimatic predictors, enhancing the model could be achieved by incorporating additional variables such as edaphic factors (soil type, pH and salinity) and a land use land cover map (LULC) in conjunction with bioclimatic variables. Additionally, it is recommended to use the Shared Socioeconomic Pathways (SSPs) from the IPCC Assessment Report 6 (AR6), an upgraded version of the Representative

Concentration Pathways (RCP), to enable more accurate forecasting of future distributions of target species. Furthermore, to mitigate sampling bias in SDMs, it is essential to incorporate random sampling techniques, integrate data from diverse sources and timeframes and use appropriate statistical methods. By applying these strategies, the robustness of models can be enhanced and more accurate predictions of species distributions can be produced. In addition, it is important to note that the uncertainty of predictions, whether past or present, tends to increase the farther away from present-day data.

Conclusion

The current study used the MaxEnt modelling method to predict the climate change impact on major NTFP species for current, future for RCP 2.6 and 8.5 (2050 and 2070) and past (mid-Holocene) climatic scenarios. The result revealed that *A. marmelos* and *T. bellirica* would be projected to experience the least impact from future climate changes; however, the habitat suitability for *B. lanzan*, *M. longifolia* and *P. emblica* is expected to decrease under RCP 8.5 (2070). The primary factor leading to reduced habitat suitability is the anticipated rise in temperature together with variability in seasonal precipitation. The assessment of the potential distribution pattern of NTFP species under rapid climatic variations plays an important role in formulating strategies for the conservation and restoration of ecosystems. By understanding how the NTFP species are likely to respond to under climatic changes, essential insights are gained into where conservation and restoration efforts should be concentrated. Overall, this approach contributes significantly to the formulation of strategic initiatives aimed at safeguarding and restoring ecosystems, considering both ecological and conservation priorities in the context of evolving climatic conditions.

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Data availability Data will be available on request.

Declarations

Ethics approval All authors have read, understood and have complied as applicable with the statement on 'Ethical responsibilities of Authors' as found in the Instructions for Authors.

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