

Habitat distribution modelling to identify areas of high conservation value under climate change for an endangered arid land tree *Tecomella undulata*

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ABSTRACT

The dryland ecosystems are fragile and have recently been subjected to paradigm shifts by climate change. To analyse this, we selected *Tecomella undulata*, an endangered arid land tree that adapts to the harsh climates of drylands. We collected 111 extant occurrence records of the species and utilised 16 environmental variables. The study identified that bio12, bio8, altitude, total nitrogen, CEC, and bio15 are the factors that significantly influence the distribution range and modelled species distribution ranges from LGM to 2100 using the Species Distribution Model. The model showed a decreased distribution from the past and predicts an increased distribution for the future. The reduced temperature and increased bio12 acted as limiting factors in the past, while the increase in bio15 and bio8 will act as enhancing factors for the future because of the warming effect due to climate change. The results predict that future climatic conditions will favour the species' distribution. Therefore, the factors which might limit the species distribution will be anthropogenic, genetic, or pest-related, which was beyond the scope of our study and needs to be identified urgently to conserve the species. The study identified priority conservation areas where environmental factors suit the species. Still, most fall outside the current conservation sites, necessitating more regional conservation sites.

1. Introduction

Climate change is a systematic change in average weather and temperature patterns over several decades (Tabari and Talaei, 2014). The global temperature increased by approximately 0.6 °C in the past century. The rate of climate change is alarming and surpasses any limit set in the last millennium (Climate Change 2001, 2001), troubling the ecosystems and organisms from diverse geographical regions. It alters the regional microclimate and makes it difficult for flora and fauna to adapt. Across the systems, the diurnal temperature ranges decreased, and the precipitation range became highly variable (Walther, G-R. et al., 2002). The changes in the structure and dynamics of each ecosystem are due to the impacts it imparted on range shifts, physiology, phenology, composition, and interaction between the elements of ecosystems. Along with anthropogenic stress, these impacts will make the already stressed ecosystems vulnerable and fragile. Several of these species are facing the threat of extinction, and some have already been wiped out (Hughes, L., 2000; Wuethrich, B., 2000; McCarty et al., 2001; Ottersen et al., 2001; Walther, G-R. et al., 2001).

A vital ecosystem that is particularly vulnerable to climate change is dryland ecosystems. The drylands house over two billion people and occupy around 40% of the land surface (N. J. Middleton, 2017). Drylands have higher evaporation rates than precipitation, including hot and cold deserts, xerophytic woodlands, savannahs, grasslands, and shrublands. The rangelands of these regions support and provide forage to approximately 50% of the world's livestock (Puigdefábregas, J, 1998) and thus form the backbone of the agropastoral economy of the majority in the global south. In India, most of the drylands are concentrated in the Northwestern region, which contains the Thar Desert and Rann of Kutch and spans mainly the states of Rajasthan, Gujarat, Haryana, Delhi and Punjab. The region is the most populated dryland region. The other significant drylands in India include the Deccan plateau, the Ladakh region and the southeastern coastal region.

The resources of drylands are exploited unsustainably (Ahmad et al., 2019; Xu et al., 2021) regardless of their limited ability to regenerate, making them highly variable and unpredictable. Many of the flora and fauna in the area are endangered due to this exploitation, and suitable habitats are becoming highly fragmented. The response of dryland to

Abbreviations: LGM, Last Glacial Maximum; SDM, Species Distribution Model; CEC, Cation Exchange Capacity; IPCC, Intergovernmental Panel on Climate Change.

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climate change in each region will be unique and influenced by climatic and non-climatic factors. In India, the Northwestern region is more sensitive to climate change than other areas due to fluctuations in precipitation and mean annual temperature (Chorran et al., 2021; Rathore and Verma, 2013). Desertification is high in the region due to the destruction of natural vegetation, unsustainable use of resources, overgrazing, overpopulation, urbanisation, and introduction of invasive alien plants. Given that most people of the region depend on agriculture, animal husbandry, and forestry, the impact of climate change on biodiversity and vegetation will adversely affect them.

The inherent dryland species are expected to proliferate and extend their range to their frontier regions (Huang et al., 2016). The situation also puts many species that live on the fringes of arid areas at risk, which will face competition from invading flora and fauna and altering climatic conditions. Even though the future climate is predicted to suit dryland species, the flora and fauna of drylands survive within their physiological limits, and slight changes in environmental factors will substantially change the habitat suitability, biodiversity, species range, and land use pattern (Archer and Predick, 2008). The unpredictable nature of dryland ecosystems necessitates using robust models to predict future habitat suitability of flora and fauna, which analyse variables from diverse spectra before concluding.

The Species Distribution Model (SDM) is a method that uses species' occurrence records to prepare correlative models with the help of GIS. The SDM is widely used to find habitat-suitability regions, overlapping niches, and species' responses to climate change (Elith and Leathwick, 2009) and to develop conservation strategies for threatened and endangered species (Spiers et al., 2018). The MaxEnt model is among the best algorithms for rare and endangered species with a few amounts of occurrence records, and it is used widely for modelling (Elith et al., 2006). The results from previous studies indicated that MaxEnt is stable and reliable, even with limited occurrence records, incomplete data sets, and gaps and can easily produce a habitat suitability map that depicts the species' range. The input data of the MaxEnt can be present only as data of the species and can be categorical and continuous. The inbuilt Jackknife test in MaxEnt can analyse each environmental variable separately. We selected MaxEnt for our research due to its clear advantages over other methods (Yi et al., 2016).

In our study, we predict the future scenarios using the SSP data from HADGEM-3 model developed by the Met Office, Hadley Centre, UK based on Assessment Report 6 of the Intergovernmental Panel for Climate Change (IPCC) to make neo-SDM. However, we took the Last Glacial Maximum (LGM) and Middle Holocene climate data from Assessment Report 5 IPCC to create paleo-SDM. The SSPs give us a comprehensive assumption on how bioclimatic variables will change in the future by including the effects of socio-political and economic aspects on the greenhouse gas emissions compared to previous RCPs (Representative Concentration Pathways), which gave limited importance to the impact of these factors in greenhouse gas emissions. The SSP values range from the minimum scenario of SSP1 to the maximum scenario of SSP5. The SSP1 deals with a sustainable green scenario where the focus is mainly on human welfare, environmental conservation, and the implementation of clean energy. However, SSP5 is the worst scenario of climate change, where the countries continue their economic development in unsustainable ways with increased dependence on fossil fuels (<https://climatedata.ca/resource/understanding-shared-socio-economic-pathways-ssps/>) (Understanding shared socio-economic pathways, 2023).

In our study, we selected *Tecomella undulata*, an arid endangered tree of Northwestern India, to analyse climate change's impact on the habitat distribution of dryland flora and fauna. The tree is an essential arid tree of the region with high ecological, economic, and medicinal value. The medium-sized tree predominantly grows in harsh environments with extreme temperatures (-20° – 50° C), low precipitation (150–500 mm) (Arshad et al., 2022) and pH (6.5–8) (Mathur and Mathur, 2023; Mathur and Mathur, 2024). The *Tecomella undulata* is used widely for wood and

traditional medicine. The wood is used to construct furniture, carvings, agriculture equipment, and toys and as a source of fuel and charcoal (Kumar et al., 2008). The species holds prime importance in environmental conservation, landscaping, and afforestation of arid regions due to its high survival rates, ability to withstand winds, and stabilisation of dunes by the network of lateral roots (Kumawat et al., 2012; Tyagi & Tomar., 2013). In its natural habitat, the species is highly mycorrhizal and acts as a nurse plant by enhancing the growth of microorganisms and enriching the soil with organic carbon and nitrogen (Rao et al., 1989; Bhau et al., 2007).

The IUCN Red Data list puts *Tecomella undulata* on the list of threatened species under criterion A2a (Plummer, 2021). The primary reasons for it becoming endangered are overexploitation, inadequate conservation efforts, and the attack of wood-degrading fungi and borers (Kalia et al., 2014). The species has a slow growth rate and limited seed viability (Kalia et al., 2014). The fertilisation rate for the species is also meagre and seldom bears fruit. The *Tecomella undulata* is a zoophilous species in which *Pycnonotus cafer* (L.) and *Pycnonotus leucotis* (Gould) act as pollinators, and *Nectarinia asiatica* acts as flower robbers (Singh et al., 2014). The equilibrium changes alter the species' germplasm quality and adversely affect their survival and regeneration capacity, making it difficult to withstand environmental changes. The vegetative propagation methods for the species using tissue culture are also not viable owing to its slow growth rate, inability to find a proper culture medium, poor field establishing rates, and root rates (Kalia et al., 2014).

As global temperatures increase and drylands expand, we expect that the future climate will be more suitable for the survival of *Tecomella undulata*. We hypothesise that the suitable habitats for *Tecomella undulata* will increase in the future compared to the limited distribution in the past when the climate was not ideal for its survival. As the distribution of the species depends on the cumulative effect of a wide range of factors, a deep analysis is needed to understand the scenarios. We also aim to identify the Priority Conservation Areas (PCAs) where the species needs to be better conserved.

2. Material and methods

2.1. Data sources

2.1.1. Species occurrence data

The occurrence records of *Tecomella undulata* were collected from different sources, including digital databases, herbarium datasets, published literature, and field visits. The databases we consulted include digital databases of the Global Biodiversity Information Facility (<http://www.gbif.org> accessed on February 28, 2023) (GBIF.org, 2023), IUCN Red List of Threatened Species (<https://www.iucnredlist.org/> accessed on March 24, 2023), and Indian Biodiversity Portal (<https://indiabiodiversity.org/> accessed on February 30, 2023) (Indian Biodiversity Portal, 2023) and herbarium databases of the Botanical Survey of India Northern Regional Centre, Dehradun (BSD) and Forest Research Institute, Dehradun (DD). The geographic location of specimens that lacked precise data was obtained through the Google Earth Pro software (version 7.3.6). The occurrence points under proximity were identified and removed, leaving us with 111 occurrence points. We obtained three fossil pollen records of *Tecomella undulata* during the Middle Holocene from published literature (Singh et al., 1974; Singh et al., 1990).

2.1.2. Environmental variables

Environmental variables are essential in determining a species' habitat suitability. To analyse the habitat suitability, we used bioclimatic variables, positional topographical variables, and edaphic factors. We downloaded the data of 19 bioclimatic variables for the Last Glacial Maximum (LGM), Middle Holocene and of SSP1 (minimum scenario of greenhouse gas emission) and SSP5 (maximum scenario of greenhouse gas emission) for future conditions of 2021-40, 2041-60, 2061-80 and

2081-100 and positional topographic variables of altitude, and aspect from the WorldClim database version 2.1 (<https://www.worldclim.org/>) (Hijmans et al., 2005). The paleo-SDMs were created for the Last Glacial Maximum (LGM) and Middle Holocene using the climate data obtained from WorldClim database 1.4 (<http://www.worldclim.org>). The bioclimatic and positional topographic variables were converted to ASCII (Brown et al., 2017) and rasterised into a spatial resolution of 30 arc-seconds (1 km) using SDM Toolbox in ArcMap 10.5.

The seven edaphic factors that we used, soil pH, bulk density (bd) of fine earth fraction, soil organic carbon stock (SOCS), proportion of clay content (CC), organic carbon density (OCD), cation exchange capacity (CEC) and total nitrogen (TN) were downloaded from Soil-Grids™ database version 2.0 (<https://isric.org/soilgrids>) (de Sousa et al., 2020). The same positional topographic and edaphic variables were used for the paleo-SDMs and neo-SDMs as they are not expected to change considerably quickly (Zhou et al., 2021).

2.1.3. Current protected areas in the predicted suitable habitats

The location data of currently protected areas in the suitable habitats of *Tecomella undulata*, like National Parks and Wildlife Sanctuaries, were collected to analyse the Priority Conservation Areas (PCAs). The list of protected areas was obtained from the websites of forest departments of Rajasthan (<https://forest.rajasthan.gov.in/content/raj/forest/en/resources/forest-statistics/general-introduction1/national-parks-and-sanctuaries-in-rajasthan.html>) (Forest Department of Rajasthan, 2023), Haryana (<https://haryanaforest.gov.in/protected-area/>) (Haryana Forest Department, 2023), Punjab (<https://forest.punjab.gov.in/en/wildlife/sanctuaries/>) (Department of Forest and Wildlife Preservation - Punjab, 2023), Delhi (<https://forest.delhi.gov.in/forest/sanctuaries>) (Department of Forest and Wildlife - Delhi, 2023), Gujarat (<https://forests.gujarat.gov.in/wildlife-sanctuaries.html>) (Gujarat Forest Department, 2023), and Tamil Nadu (https://agritech.tnau.ac.in/forestry/forestry_eco_wildlife_sanctuaries.html) (Forestry, 2023). The geographic location of the areas was obtained through the Google Earth Pro software (version 7.3.6). The layer that contains the location data was overlaid on the SDM of current suitable habitats to get a clear picture of Priority Conservation Areas (PCAs).

2.2. Variable selection

Our study determined each variable’s Pearson correlation coefficient (r) to eliminate multicollinearity between variables, analyse cross-correlation between variables and select variables with more predictive power (Supplementary file 1) (Yi et al., 2016). The variables having

a Pearson correlation coefficient ≥ 0.8 were removed from the analysis (Wei et al., 2018) to obtain nine bioclimatic variables (bio1, bio2, bio3, bio4, bio8, bio9, bio12, bio14, bio15, bio18, bio19), two positional topographic variables (altitude, and aspect) and three edaphic variables (bulk density, cation exchange capacity, and Total Nitrogen). The selected variables are listed below in Table 1.

2.3. MaxEnt model & its validation

The algorithms used for the SDM fall under two subfields: regression-based approaches and machine learning. The regression-based methods include multivariate adaptive regression splines (MARS) and generalised linear and additive models. The machine learning approach includes Maximum Entropy (MaxEnt), Random Forest, genetic algorithms, Artificial Neural Networks (ANN), and Classification Trees (CARTs) (Mathur and Mathur, 2023). Therefore, selecting a suitable algorithm for our work is very important. The model that provides the appropriate range for the species under study should be chosen. Our study used the MaxEnt model, which is among the best SDM algorithms.

The MaxEnt is a Java-based software developed by Philips et al. (2006) based on the Maximum Entropy theory proposed by Jaynes in 1957 (Jaynes, 1957). The occurrence records and environmental variables for the species were imported to the MaxEnt model (version 3.4.4) (<http://www.cs.princeton.edu/>) to prepare the SDM. The Maxent plots the Receiver Operating Curve (ROC), which calculates the performance of the model by computing the coordinate points (in the x-axis (1 – specificity = false positive rate) and y-axis sensitivity) at all cutoff points where the results are determined. The model’s accuracy is high if the curve is closer to the upper left corner as the sensitivity and specificity = 1. The value gives an Area Under the Receiver Operating Curve (AUC) value, generally between 0.5 and 1, a measure of the model’s overall performance (Peterson et al., 2008). The model’s overall performance is better when the AUC value is high. An AUC value of 0.5–0.6 is considered failed, 0.6–0.7 poor, 0.7–0.8 fair, 0.8–0.9 good, and 0.9–1 excellent (Li et al., 2020). The AUC has a low risk of bias unless there are very few data points. For our model, 75% of sample data were randomly considered as training data and 25% as testing data, and the replicates were run ten times to obtain the average AUC value (Waheed et al., 2023, 2024a).

The contribution of each variable and the importance of permutation to the distribution model of *Tecomella undulata* is determined using a Jackknife test. The regularised test gain of the Jackknife test represents how the presence data of MaxEnt analysis synchronises with the uniform distribution. The dark blue bars represent the gain of each variable when

Table 1
Environmental variables used to analyse the distribution of *Tecomella undulata* in this study.

Categories	Sources	Variables	Abbreviation	Units	Scaling Factor
Edaphic	Soil-Grids™ https://isric.org/soilgrids	Bulk density	bd clipped	g cm ⁻³	100
		Cation Exchange Capacity	CEC_india		10
		Total Nitrogen	N_india		10
Positional Topographic	WorldClim- Global Climate Data http://www.worldclim.org	Altitude	Alt.	m	1
		Aspect	Asp.	Degree	
Bioclimatic		Annual Mean Temperature	bio1	°C	1
		Mean Diurnal Range (Mean of monthly max temp-min temp)	bio2	°C	1
		Isothermality	bio3	No dimension	100
		Temperature Seasonality	bio4	100	1
		Mean Temperature of Wettest Quarter	bio8	°C	1
		Mean temperature of the driest quarter	bio9	°C	1
		Annual Precipitation	bio12	mm	1
		Precipitation of Driest Month	bio14	mm	1
		Precipitation Seasonality (Coefficient of Variation)	bio15	No dimension	100
		Precipitation of Warmest Quarter	bio18	mm	1
Precipitation of Coldest Quarter	bio19	mm	1		

used in isolation, while the light blue bars depict the loss to the model when the variable is removed (Yi et al., 2016).

2.4. Response curves

The response curves represent the logistic relationship between the suitable habitats and the environmental variables in a simplified manner (Yi et al., 2016). The curves graphically depict how each environmental

variable influences the Maxent prediction while keeping the value of all other variables at their average sample value. The model takes the effect of all the variables together to predict the probability of presence. The MaxEnt software prepared the response curves of 14 environmental variables influencing habitat suitability and prepared the model. The model took the mean response curve of 10 replicate runs of Maxent and the mean ± one standard deviation. The inference of the graphical depiction of response variables gives a better understanding of the

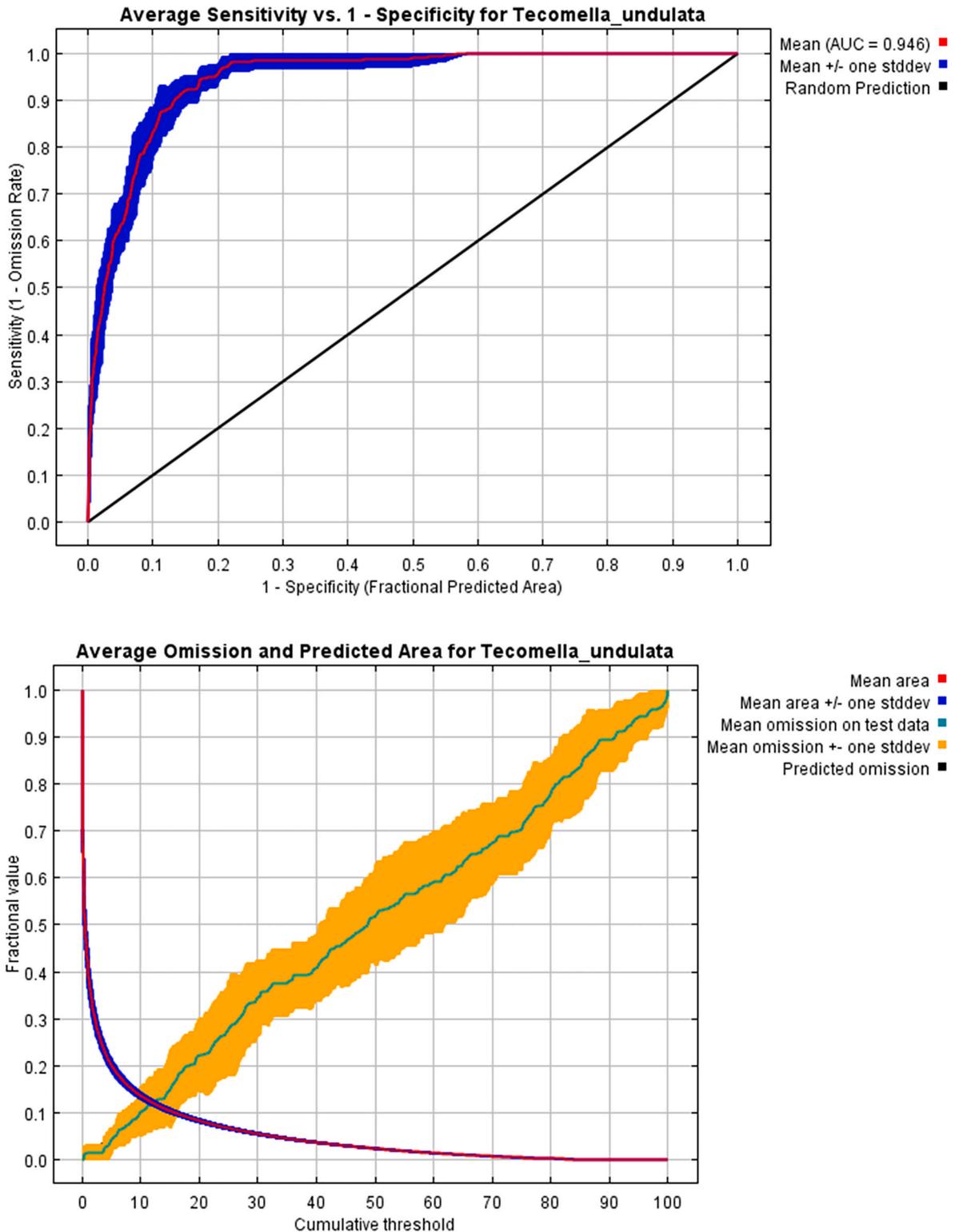


Fig. 1. Reliability test of the distribution model created for *Tecomella undulata*.

suitable range for the species' growth in each variable.

2.5. Area change calculation

The regions with the possible existence of *Tecomella undulata* were predicted using the average MaxEnt output ranging from 0 to 1. The previous studies identified that the segregation of the prediction range with five equal-sized probability classes would provide a vivid analysis (Waheed et al., 2023, 2024b). The suitable habitats of *Tecomella undulata* were divided into five equal parts, namely no suitable, low suitable, moderately suitable, highly suitable and extremely suitable, using Reclassify in Spatial Analyst Tool of ArcMap 10.5 software for each model from past, present, and future. The no suitable regions were identified for a range between 0.2 and 0.4, low suitable regions for a range between 0.4 and 0.8, moderately suitable for a range between 0.4 and 0.6, highly suitable for a range between 0.6 and 0.8 and extremely suitable for a range between 0.8 and 1 (Waheed et al., 2023).

The extent of the area of suitable habitats in each Species Distribution Model from past, present, and future were calculated using the ArcMap 10.5 software. The extent of the area in each model is compared to the present model, and changes for each case are determined. The analysis of changes in the importance of suitable habitats will help to analyse how climate influences habitat suitability and to predict the priority conservation areas for the concerned species.

3. Results

3.1. Model performance and contribution of environmental variables

The calculated ROC of the predicted MaxEnt showed an AUC value of 0.946, which is considered a good model performance (Fig. 1). The model predicted the distribution range of *Tecomella undulata* very well. The model predicted a higher percentage contribution in the model for bio12, alt, TN, CEC, and bio15 (Table 2). Subsequently, the Jackknife test (Fig. 2) showed that bio12, bio8, TN, bd, and bio2 provided high gains (>0.6) when used in isolation, indicating that these are the most influential factors for the distribution of *Tecomella undulata*. Other variables only had low yields when used in isolation.

3.2. Response of variables towards suitable habitat

The response curves (Supplementary File 2) show how environmental variables are related to the species' habitat suitability. The model predicts that the suitable conditions for *Tecomella undulata* are warm and dry, and the increase in precipitation affects it negatively. The annual rainfall (bio12) has a higher percentage contribution in the model of 44%. The model predicts that the suitable range of annual precipitation

Table 2
Contribution of environmental variables to the SDM.

S. No	Variable	Percent contribution	Permutation importance
1.	bio12	44.8%	38.4
2.	Altitude	12.9%	7.2
3.	Total Nitrogen	11.7%	0.2
4.	CEC	11.1%	2.5
5.	bio15	7.6%	12.3
6.	bio9	3.4%	3.1
7.	bio8	3%	21.1
8.	bio1	1.6%	0.5
9.	Aspect	1.4%	0.6
10.	bio2	0.9%	4.9
11.	bio3	0.5%	5
12.	Bulk density	0.4%	0.4
13.	bio14	0.3%	0.9
14.	bio4	0.2%	2.6
15.	bio18	0.1%	0.3
16.	bio19	0	0.1

for the growth of *Tecomella undulata* is less than 100 mm/year. The model predicts that the mean temperature of the wettest quarter (bio8) also has a strong influence with high permutation importance and prefers temperatures between 27 °C and 33 °C during monsoons. The precipitation seasonality (bio15) has a moderate influence (7.6 % per cent contribution) on the distribution model. The *Tecomella undulata* is found to prefer regions with bio15 greater than 1.2.

The topographic variables and edaphic variables also contribute significantly to the model. The most prominent among them are altitude (12.9%), total nitrogen (11.7%), and cation exchange capacity (11.1%). The apt altitude for the growth of *Tecomella undulata* lies in a range of 150m–600m. Even though some trees are found beyond this range, the density of the species is less in those regions. The preferred values for nitrogen content are less than 20 mg/kg of soil, and CEC is less than 20 meq/100g, which generally falls in the range of acidic sandy soil, the most abundant soil of the drylands of Northwestern India. The other environmental variables contribute little to the model.

3.3. Prediction of suitability for distribution in past, present, and future climate change scenarios

The Species Distribution Model (SDM) under current climatic conditions (Fig. 3) shows a moderate to high habitat suitability for *Tecomella undulata* in the drylands of Northwestern India, comprising Rajasthan, Haryana, Delhi, and Punjab. Most occurrence records were also obtained from this region. Moderate habitat suitability regions for *Tecomella undulata* also exist in the Kutch and Saurashtra regions of Gujarat and the South and Kongunadu regions of Tamil Nadu. The suitable habitats of these regions are isolated from each other and highly fragmented. The extent of extreme and highly suitable habitats at present is 52,186.74 km² and 28,975.27 km², which is high compared to the past models of the LGM and the Middle Holocene (Table 3).

The SDMs developed for two past scenarios of the Last Glacial Maximum (LGM) and the Middle Holocene predict a limited distribution for the species in the past (Fig. 4). The model for LGM shows the presence of primarily low-suitable regions in Northwestern India in the west and northwest of the Aravalli. The suitable habitats for *Tecomella undulata* are utterly absent in other regions, including Gujarat and Tamil Nadu. The extreme and highly suitable habitats were reduced to 0.004% and 0.24% of the total area and were represented only by 147.84 km² and 1167.82 km². The extent of suitable habitats increased while coming to the Middle Holocene compared to the LGM (7962.78 km² for extremely suitable habitats and 12,401.64 km² for highly suitable habitats), but still a considerably low value compared to the current situation (approximately one-fourth of both extreme and highly suitable habitats compared to present model). The suitable habitats of *Tecomella undulata* during the Middle Holocene concentrated mainly in the Thar desert and showed a westward shift from the suitable habitat in the model for LGM. During the Middle Holocene, suitable habitats were also absent in other parts of India.

For the future, we prepared models for 2021-40 (Fig. 5), 2041-60 (Fig. 6), 2061-80 (Fig. 7), and 2081-100 (Fig. 8) under the minimum (SSP1) and maximum climate change scenarios (SSP5). Future models predict that suitable habitats will continue to be concentrated more in Northwestern India. At the same time, an increase in suitable habitats for the future is also visible in Gujarat for SSP1 and SSP5. The increase in suitable habitats is more visible in Kutch and northern regions that are proximal to the drylands of Rajasthan, whereas only a marginal change happens in Saurashtra. In Tamil Nadu, the suitable habitats are predicted to remain almost constant in the SSP1 scenario, while in the SSP5 scenario, the suitable habitats decrease and nearly vanish by 2081-100.

Both the SSP1 and SSP5 predict an increase in extreme (2.46% for SSP1 and 2.66% for SSP5) and highly (0.78% for SSP1 and 0.68% for SSP5) suitable habitats from the current situation to 2021-40. The increase in suitable habitats is more prominent in SSP5 than in SSP1. In the SSP1 scenario, the extremely suitable habitats increase till 2041-60 to

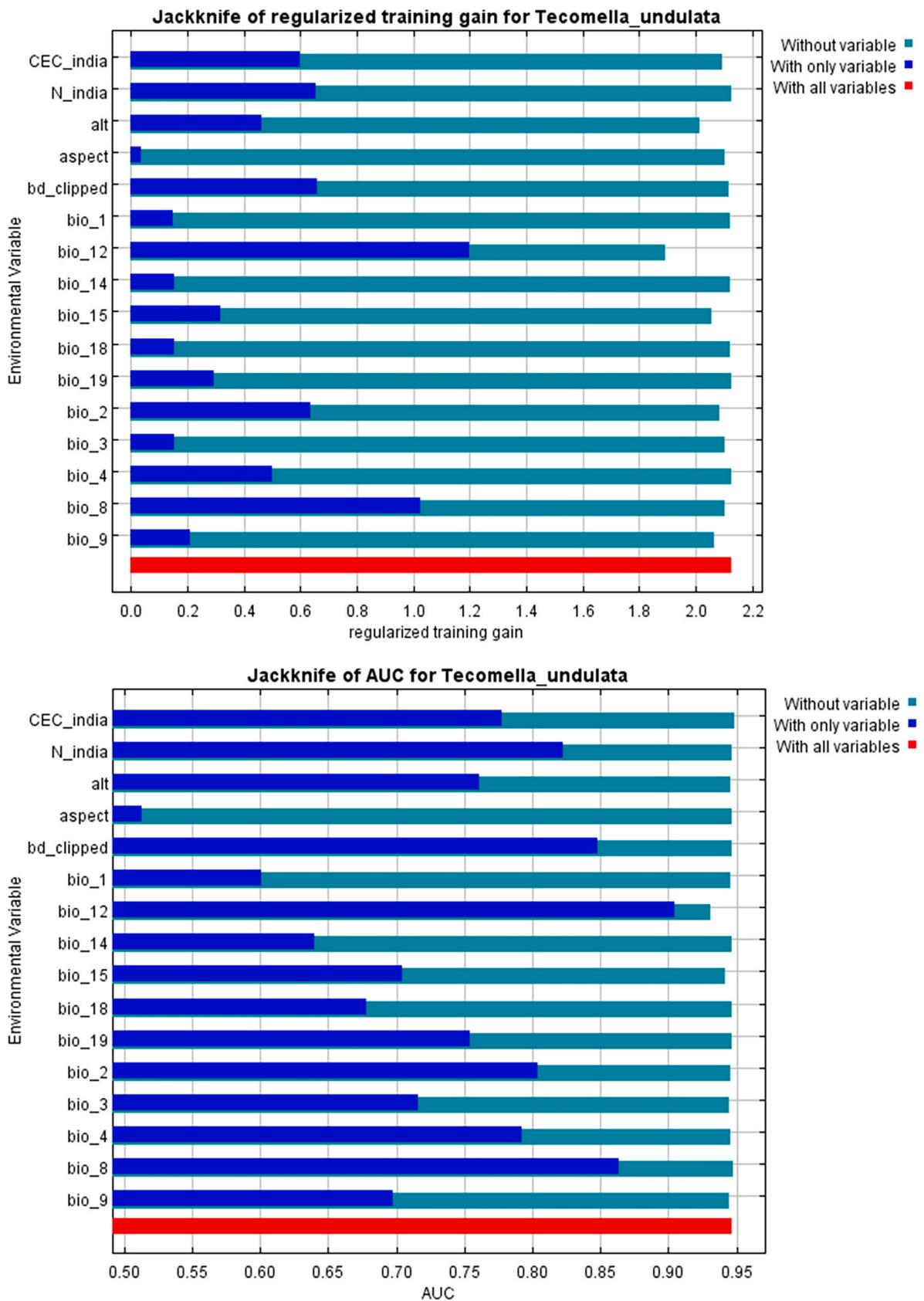


Fig. 2. The results of the jackknife test of variables's contribution in modelling *Tecomella undulata*'s habitat distribution.

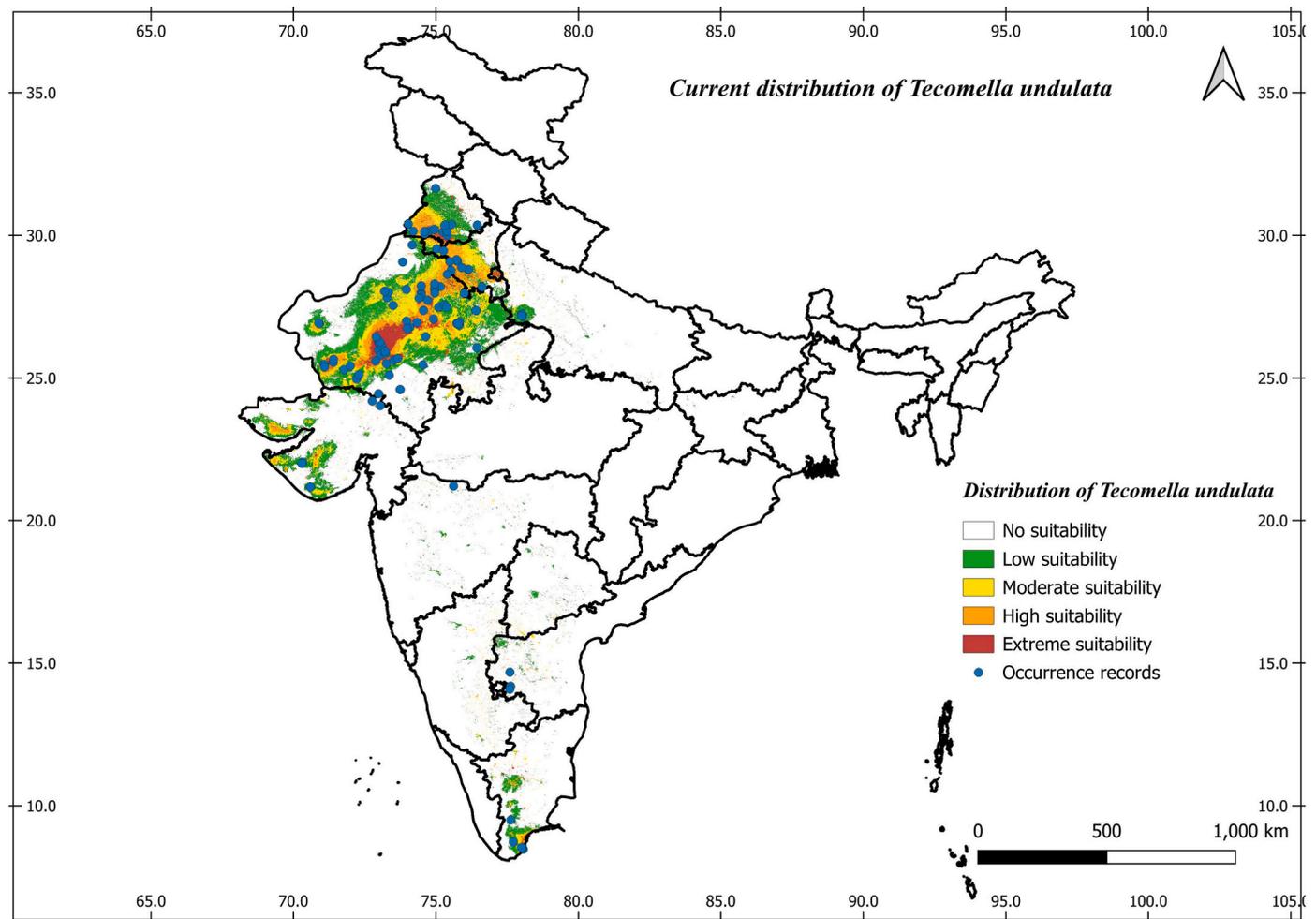


Fig. 3. Map showing the current species distribution of *Tecomella undulata*.

120,029.4 km² and then show a decrease (93,499.49 km² in 2080-100), while highly suitable habitats show an increasing trend till 2081-100 (102,014.58 km²). The SSP5 scenario predicts that the extreme and highly suitable habitats will continue to increase till 2081-100. The rate of increase in suitable habitats after 2021-40 for highly suitable habitats is less, while the extremely suitable regions continue to increase at a high rate. The highly suitable habitats will increase by 0.96%–83,943.96 km², and extremely suitable habitats will increase by 4.74% to reach an extent of 184,867.89 km² in 2081-100. The model predicts a significant increase in suitable habitats during 2021-40. The model's prediction synchronises with the concept that the upcoming warming climate will favour the proliferation of dryland species.

4. Discussion

Tecomella undulata is a dryland species that prefers warm, dry climatic conditions. The species mainly depends on a lesser amount of annual precipitation and is affected significantly by the changes in precipitation seasonality. In this study, we discuss the changes in the spatial pattern of suitable habitats by creating SDMs during different time frames from the LGM to 2100. The models provide a scientific basis for identifying the Priority Conservation Areas (PCAs) and proper utilisation and management of the species. The study identified factors that considerably influence the growth of the *Tecomella undulata*.

4.1. Current distribution of *Tecomella undulata*

The current distribution of *Tecomella undulata* is mainly concentrated in Northwestern India, with some patchy fragmented distribution in Gujarat and Tamil Nadu. Most extant occurrence records also belong to the Northwestern region of India; a few are from south Tamil Nadu. The bioclimatic factors that discern suitable habitats are annual precipitation (bio12) and precipitation seasonality (bio15). The recent change in weather patterns in Northwestern India showed erratic rainfall with increased temperatures. Even though the erratic rainfall harmed the natural vegetation (Shekhawat et al., 2012), it increased precipitation seasonality in the region. It did not alter the annual mean precipitation of the region much, which is a favourable scenario for *Tecomella undulata*. The increase in temperature, significantly the increase in bio8, also favoured the distribution of the species in current times. The cumulative effect of bio8 and bio15 created a favourable situation for *Tecomella undulata* in Northwestern India.

The present suitable habitats for *Tecomella undulata* in Gujarat and Tamil Nadu show an increase compared with past models for the LGM and the Middle Holocene. The increase in suitable habitats in Gujarat is because of the increase in drylands due to the upliftment of Kutch (Burnes, 1834) and the disappearance of ancient rivers like Saraswati due to the increased aridness (Saini et al., 2020). The formation of suitable habitats in southern Tamil Nadu was due to the reduced precipitation rate and increased sand deposition by dry wind blowing from the coastal region (Alappat et al., 2016).

The edaphic factors of total nitrogen and cation exchange capacity

Table 3
Suitable Habitat distribution of *Tecomella undulata* in current, Mid-Holocene, and future scenarios.

Range	Habitat suitability	Current (Km ²) (%)	LGM (Km ²) (%) (Δ%)	Middle Holocene (Km ²) (%) (Δ%)	SSP1_2021-40 (Km ²) (%) (Δ%)	SSP5_2021-40 (Km ²) (%) (Δ%)	SSP1_2041-60 (Km ²) (%) (Δ%)	SSP5_2041-60 (Km ²) (%) (Δ%)	SSP1_2061-80 (Km ²) (%) (Δ%)	SSP5_2061-80 (Km ²) (%) (Δ%)	SSP1_2081-100 (Km ²) (%) (Δ%)	SSP5_2081-100 (Km ²) (%) (Δ%)
0-0.2	Not suitable	2,957,212.1 (89.95)	3,223,605.54 (98.05) (8.1)	3,212,399.63 (97.71)(7.76)	2,868,501.99 (87.25) (-2.7)	2,882,793.91 (87.69) (-2.26)	2,847,251.47 (86.6) (-3.35)	2,834,738.26 (86.22) (-3.73)	2,857,549.91 (86.92) (-3.03)	2,831,205.03 (86.12) (-3.83)	2,840,886.08 (86.41) (-3.54)	2,834,066.01 (86.2) (-3.75)
0.2-0.4	Low suitable	165,060.41 (5.02)	50,944.53 (1.55) (-3.47)	38,313.23 (1.16) (-3.86)	143,354.29 (4.36) (-0.66)	123,637.94 (3.76) (-1.26)	145,237.13 (4.42) (-0.6)	127,197.2 (3.87) (-1.15)	138,521.21 (4.21) (-0.81)	106,425.53 (3.24) (-1.78)	143,675.07 (4.37) (-0.65)	102,624.52 (3.12) (-1.9)
0.4-0.6	Moderately suitable	84,199.66 (2.56)	3350.99 (0.1) (-2.46)	16,556.9 (0.5) (-2.06)	84,672.92 (2.57) (0.01)	85,666.88 (2.61) (0.05)	96,568.75 (2.78) (0.38)	91,489.27 (2.78) (0.22)	94,791.91 (2.88) (0.32)	83,130.39 (2.53)(-0.03)	103,280.03 (3.14) (0.58)	77,852.86 (2.37)(-0.19)
0.6-0.8	Highly suitable	52,186.74 (1.59)	1167.82 (0.03) (-1.56)	12,401.64 (0.38)(-1.21)	78,052.77 (2.37) (0.78)	74,697.13 (2.27) (0.68)	74,268.49 (2.26) (0.67)	82,408.87 (2.5) (0.91)	84,041.59 (2.56) (0.97)	83,264.28 (2.53) (0.94)	102,014.58 (3.1) (1.51)	83,943.96 (2.55) (0.96)
0.8-1	Extremely suitable	28,975.27 (0.88)	147.84 (0.004) (-0.876)	7962.78 (0.24) (-0.64)	108,773.27 (3.31) (2.46)	116,559.39 (3.54) (2.66)	120,029.4 (3.65) (2.77)	147,521.65 (4.49) (3.61)	108,450.63 (3.3) (2.42)	179,330.01 (5.45) (4.57)	93,499.49 (2.84) (1.96)	184,867.89 (5.62) (4.74)

Total Area - 3,287,634.18.

% - Given Area/Total Area.

Δ% - Percentage for given model - Percentage at current situation.

significantly affect the distribution. The increased temperature with precipitation seasonality reduces soil nitrogen and cation exchange capacity (Fang et al., 2017; Brevik, 2013; Joseph et al., 2018). The increased soil erosion due to erratic rainfall also reduced the soil nitrogen and cation exchange capacity (Chiew et al., 1995; Brevik, 2013; Fang et al., 2017), making the soil preferable for the growth of *Tecomella undulata*. The soil erosion in the region due to rainfall and wind is amplified by the loss of vegetation cover (Middleton, 2017) due to deforestation, overgrazing and forest fires, which shows how human disturbance impacts species distribution. The increased mining, unsustainable irrigation in drylands and conversion of rangelands and barren areas into croplands also reduce the soil nitrogen content and CEC. The release of effluents from industries that contain NO₂ and N₂O into the atmosphere and water bodies increases soil nitrogen and CEC (Brevik, 2013). The unsustainable use of artificial fertilisers and pesticides also increases soil nitrogen and CEC (Brevik, 2013). The increased industrialisation and cultivation in the drylands of Northwestern India is, therefore, a significant concern for the survival of *Tecomella undulata*. The study did not analyse the impact of anthropogenic influence on the distribution of the species, but it is profound through its effect of altering the edaphic factors. As the species is getting endangered, even though the climate supports its growth, it shows that the anthropogenic influence is affecting the species negatively. More studies need to be done to understand how anthropogenic factors affect the native vegetation of drylands in Northwestern India.

4.2. Distribution of *Tecomella undulata* in the past

The Species Distribution Model (SDM) for the Last Glacial Maximum (LGM) time predicts a lesser extent of suitable habitats for the growth of *Tecomella undulata* (1167.82 km² of area for highly suitable habitats and 147.84 km² of area for extremely suitable habitats). The suitable habitats mainly were of low suitability (165,060.41 km²) and were confined to the west and northwest of Aravalli. During the LGM, the region experienced a cold, dry climatic condition (Tejavath et al., 2020) with low values of bio8, making the area less suitable for the growth of *Tecomella undulata*. The aeolian activity was also less during the LGM (Sinha et al., 2006). Even though the climate was drier during the LGM, it was different from today, which had a cold temperature, which is not suitable for the growth of *Tecomella undulata*. The drier regions were towards the eastern part of the region as channels of paleo-river Saraswati were flowing through the western part, which disappeared around 10 Ka between 18 ka and 11.6 ka due to the loss of tributaries and uplift of Shivalik ranges (Saini et al., 2020).

The SDM we obtained correlates with earlier studies in the region during the Middle Holocene (Singh et al., 1974, 1990). The SDM model predicts that the suitable habitat for *Tecomella undulata* during that time was lesser and confined mainly to the western part of Rajasthan compared to the present condition where the suitable habitat is present in most regions of Northwestern India. The reduction in the distribution of suitable habitats compared to the present-day scenario during the Middle Holocene was mainly due to the increased precipitation. The region received annual precipitation twice that of modern value during the Middle Holocene period, primarily attributed to increased winter precipitation, which was also validated through pollen analysis (Singh et al., 1974, 1990). The increase in suitable habitats compared to the LGM can be attributed to the rise in bio8, which favoured the growth of *Tecomella undulata*. The suitable habitats may have shifted towards the west as the western region got drier due to the drying up of the Saraswati River and increased aeolian activity there (Saini et al., 2020).

The fossil pollen records for *Tecomella undulata* of the Middle Holocene were obtained from a literature review of previous studies conducted in three paleolakes of Pushkar, Sambhar, and Didwana (Singh et al., 1974, 1990), which are not suitable habitats. The pollen got transported from suitable habitats to the lakes as *Tecomella undulata* is pollinated by *Pycnonotous cafer* (L.) and *Pycnonotous leucotis* (Gould)

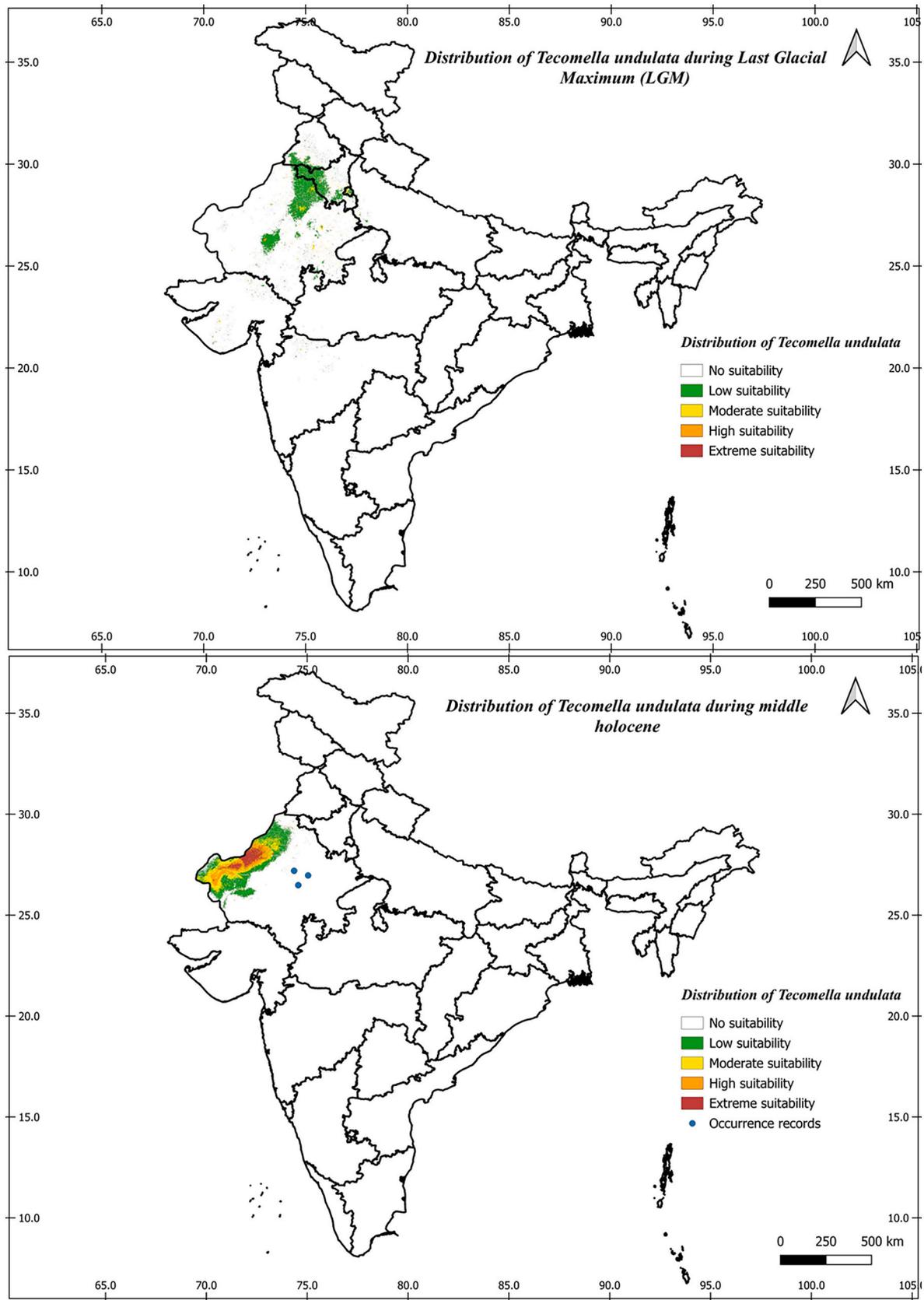


Fig. 4. Map showing species distribution of *Tecomella undulata* during the past.

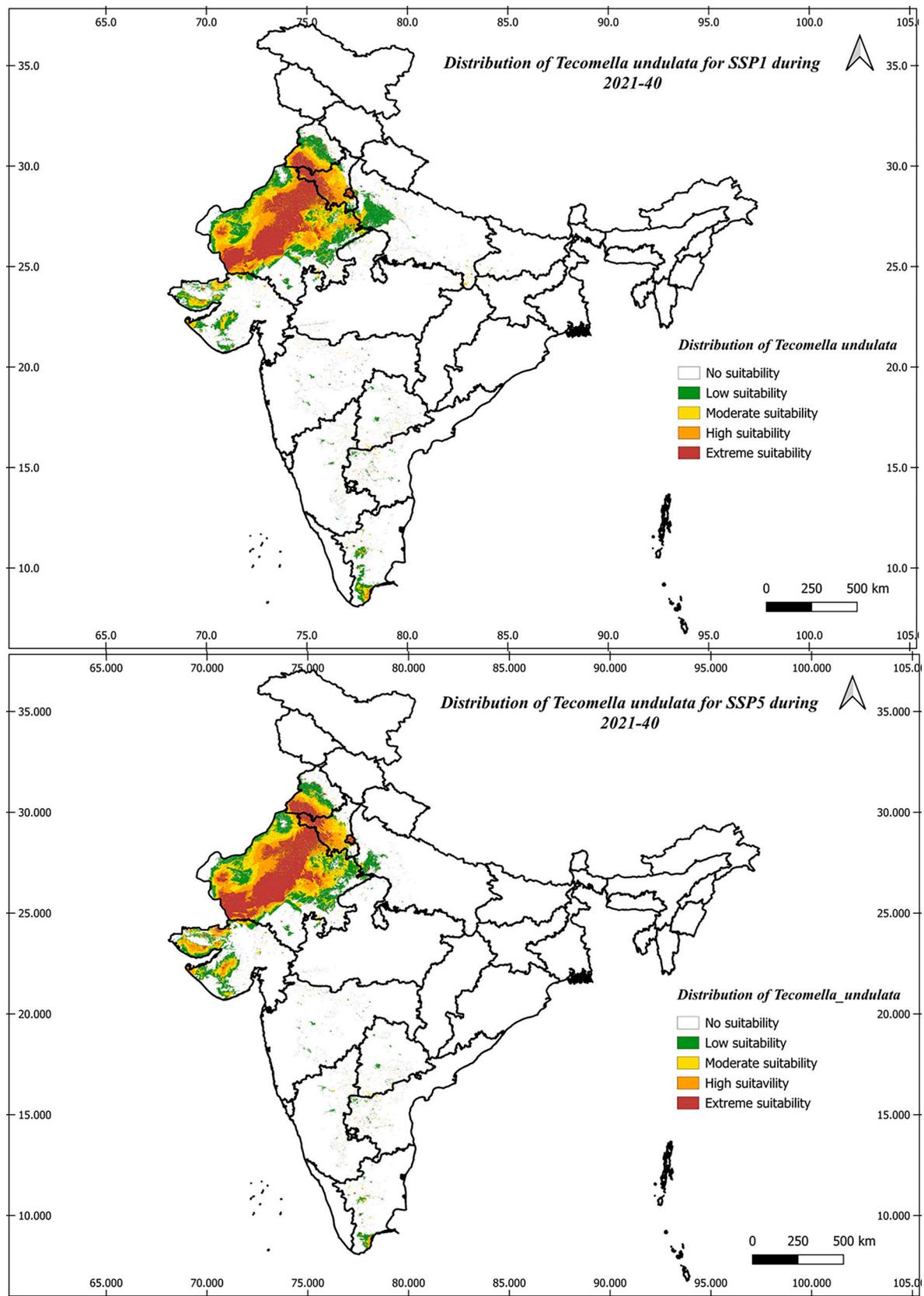


Fig. 5. Map showing species distribution of *Tecomella undulata* during 2021-40.

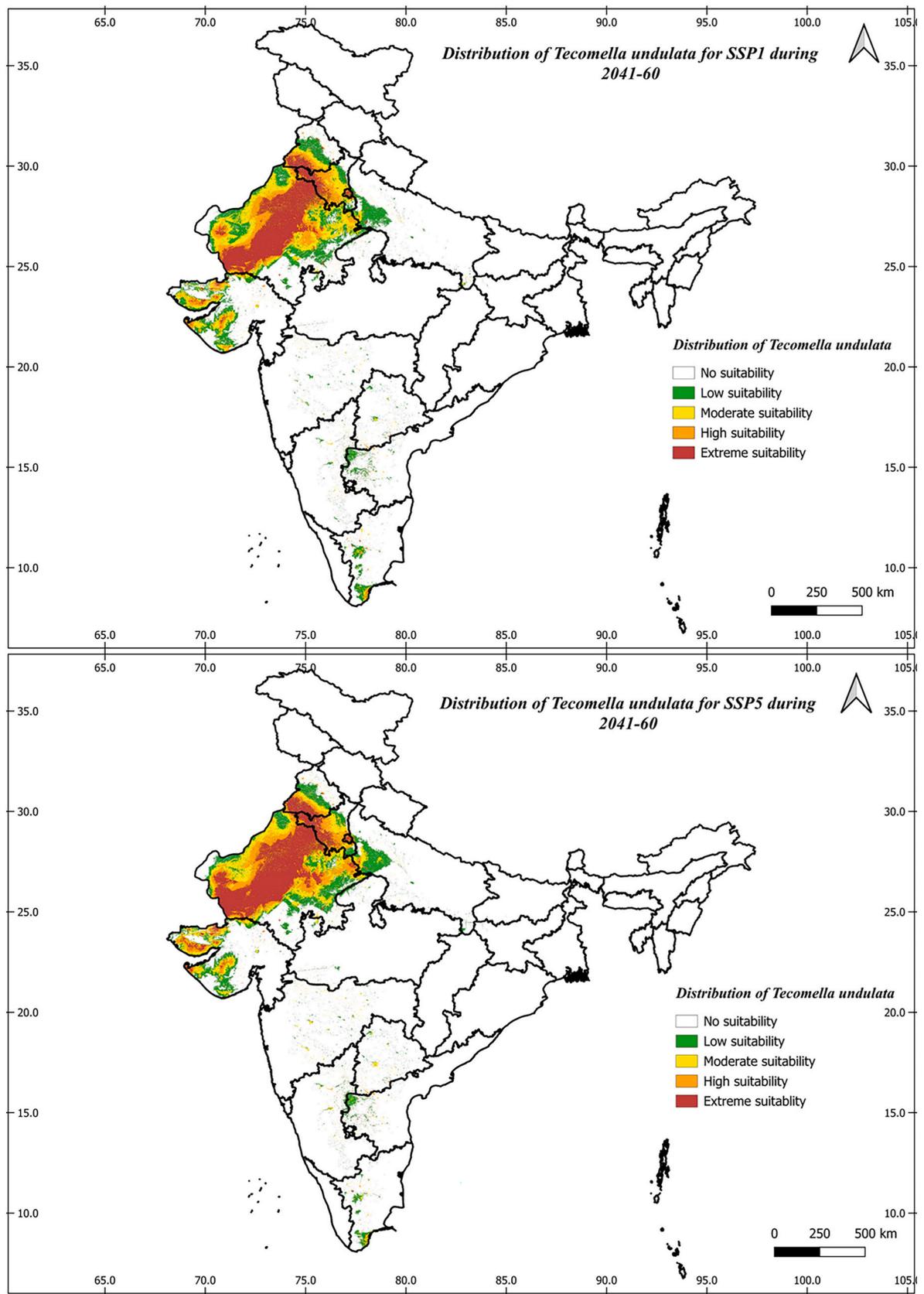


Fig. 6. Map showing species distribution of *Tecomella undulata* during 2041-60.

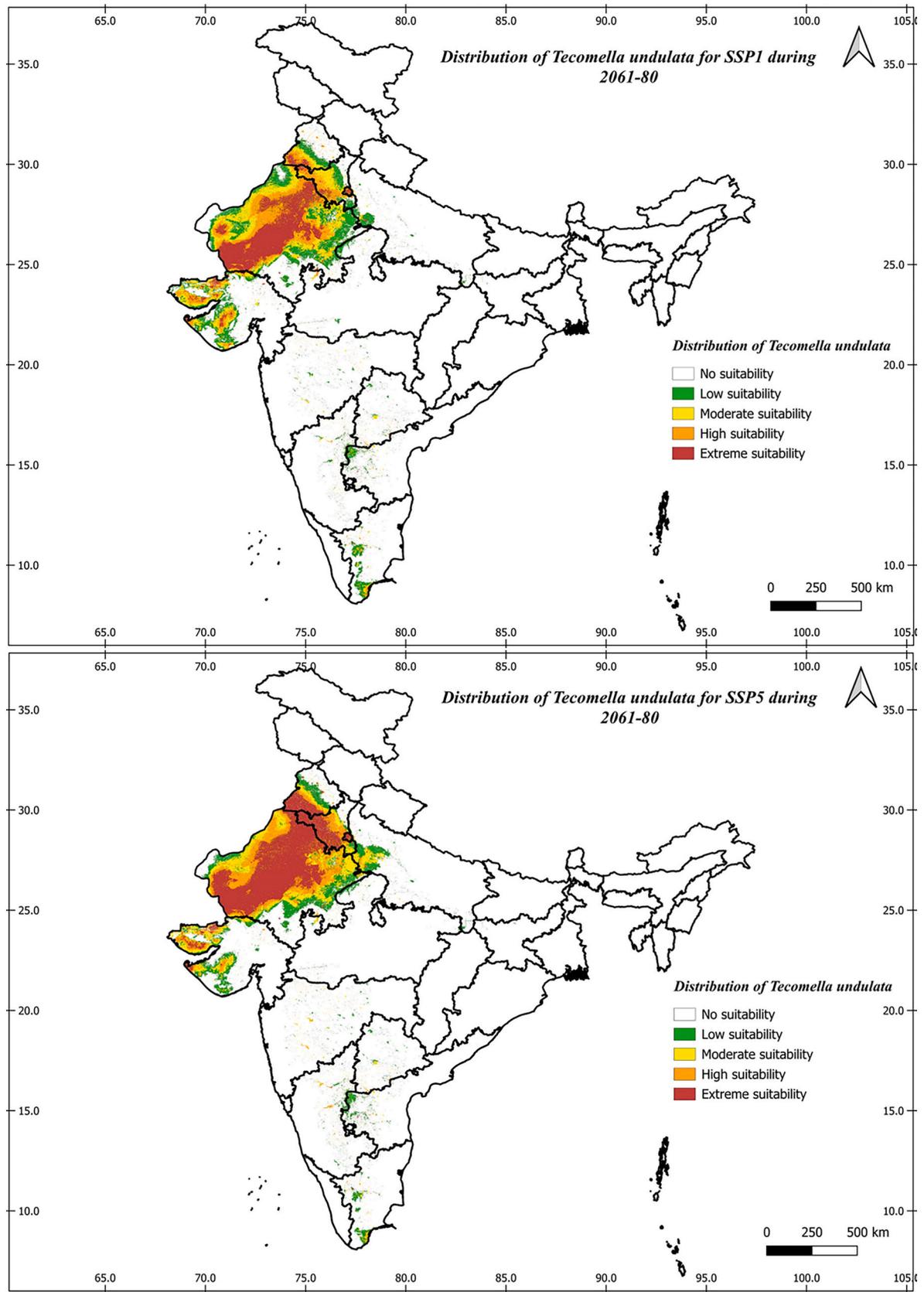


Fig. 7. Map showing species distribution of *Tecomella undulata* during 2061-80.

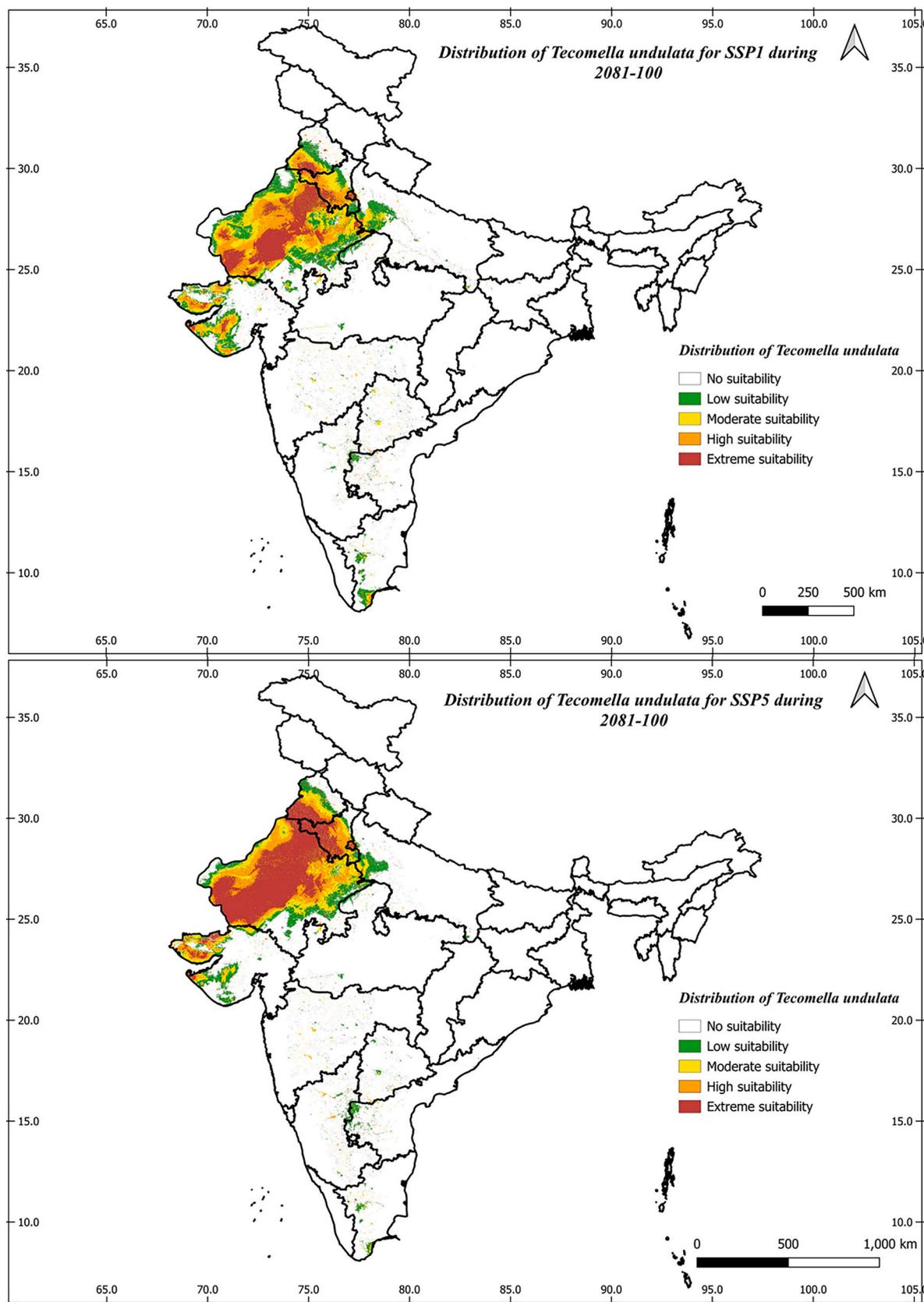


Fig. 8. Map showing species distribution of *Tecomella undulata* during 2081-100.

(Singh et al., 2014). Even though the lakes fall outside suitable habitats of *Tecomella undulata*, they are well within reach of these birds who might visit the lakes for drinking water. The pollen of dry areas has a low masking factor and can get transported to distant places through wind or water (Horowitz, 1992) as the region has poor vegetation.

4.3. Impact of climate change on future distribution of *Tecomella undulata*

Future models predict that the suitable habitats for *Tecomella undulata* will continue to be concentrated more in Northwestern India. The results from the SDMs predict an increase in the suitable habitats of *Tecomella undulata* up to 2100 in both SSP1 and SSP5 climate change scenarios. The increase in suitable habitats is mainly predicted to happen during 2021-40 when the extreme and highly suitable habitats are expected to increase substantially both in SSP1 and SSP5 (an increase in area of about three times for extremely and half times for highly suitable habitats). In extremely suitable habitats for SSP1 and SSP5 scenarios of 2021-40, it is expected to increase by almost three times its current area, showing that *Tecomella undulata* favours growing in a climate with warmer dry temperature conditions and erratic precipitation. The increase in suitable habitats can be mainly attributed to the predicted warming effect due to global climate change, which can increase the value of bio8 and bio15. The model for 2041-60 also predicts an increase in suitable habitats (extremely suitable habitats of 120,029.4 km² in SSP1 and 147,521.65 km² in SSP5), but the rate of increase is less compared to the model of 2021-40. The models after 2041-60 predict a different behaviour in SSP1 and SSP5. In SSP1, after 2041-60, the trend shows a reduction in extremely suitable habitats (93,499.49 km² in 2081-100) even though it is marginal, while in SSP5, it predicts a continued increase (184,867.89 km² in 2081-100). The models predict that the maximum influence of climate change will affect *Tecomella undulata* during 2021-40, and after that, it will be able to maintain its range of distribution. So, 2021-40 is suitable from the climate change perspective and is crucial to implementing our conservation efforts to increase the distribution.

Even though the annual precipitation is expected to increase in North India (Saini et al., 2022; Mishra et al., 2020), in the drylands of Northwestern India, it will be more erratic (increased bio15) which favours the growth of *Tecomella undulata*. The model predicts that the number of suitable habitats in Gujarat will also increase. The increase of suitable habitats in Gujarat is visible mainly in the SSP1 scenario, while in SSP5, the extent of suitable habitats is almost constant. The reason for these changes in suitable habitats for *Tecomella undulata* in Gujarat is similar, as the region lies proximal to Northwestern India. For Tamil Nadu, the suitable habitats appear to be not affected much by climate change in SSP1, while in SSP5, it negatively affects the suitable habitats. The situation in Tamil Nadu is different as the general trend predicts an increase in suitable habitats for *Tecomella undulata*. The distribution of *Tecomella undulata* in the Tamil Nadu region is mainly influenced by annual precipitation, and an increase in annual rainfall for the future in the area (Yaduvanshi et al., 2019) negatively affects the extent of suitable habitats.

4.4. Priority conservation areas for *Tecomella undulata*

Tecomella undulata is currently an endangered species. The species can be conserved by setting up priority conservation areas like national parks, wildlife sanctuaries, and conservation centres where human activity is regulated. Presently, there are very few conservation efforts for the species, and our study identified conservation areas for other species set up in the habitat-suitable regions of *Tecomella undulata* that can be used to preserve the species. The conservation sites in high and extremely suitable habitats of *Tecomella undulata* include Desert National Park, Tal-Chapar Wildlife Sanctuary, Todgarh-Raoli Wildlife Sanctuary, Sariska National Park, Nahargarh Wildlife Sanctuary, Jamwa

Ramgarh Wildlife Sanctuary, Abohar Wildlife Sanctuary, Abubshahar Wildlife Sanctuary, Nahar Wildlife Sanctuary, Bhindawas Wildlife Sanctuary, Asola Bhati WLS, Sultanpur National Park, Gaga Wildlife Sanctuary, Rampara Wildlife Sanctuary, and Gir National Park. The Vallanadu Wildlife Sanctuary in south Tamil Nadu lies in low suitable habitats of *Tecomella undulata*. However, it can be considered a Priority Conservation Area (PCA) as it contains suitable habitats for *Tecomella undulata* in South India. Most of the suitable habitats lie outside the conservation areas, which necessitates setting up more conservation areas to preserve *Tecomella undulata*.

4.5. Limitations of the study

The models predict a road of recovery for *Tecomella undulata* from its endangered status. The study results are solely based on the environmental variables, although several other factors influence the suitable habitats and growth of *Tecomella undulata*. The significant factors to be considered include anthropogenic influence, physiological and genetic limitations of the species, and changes in edaphic factors and landscape patterns. Even though future environmental factors favour the distribution of the species, we are still determining the impact of other limiting factors, as they are beyond the scope of our current study. In many situations, the effect of these factors overwhelms the favourable scenarios created by environmental factors, making the distribution trend go against our predictions.

The unsustainable use to obtain timber, firewood, and fodder for cattle is the primary factor influencing the *Tecomella undulata* distribution. Overusing the species creates a situation where superior individuals are utilised, and only inferior ones survive. The overuse of the species produces a bottleneck effect, which selects inferior varieties, leading to a depletion in the gene pool (Kumar et al., 2017). The selected inferior species might not have the physiological adaptations to adapt to environmental changes.

The physiological and genetic pattern of *Tecomella undulata* also took a considerable time to evolve. The reproductive method of the plant, particularly the phenology of pollination, shows significant dependence on environmental patterns as they are adapted to the timing of the arrival of pollinators. Irregular fertilisation changes the species' genetic makeup by changing the ploidy and reducing the fruiting and seed viability (Kumar et al., 2017). *Tecomella undulata* is a slow-growing tree that requires considerable time to mature. Therefore, the harmful effects of genetic and physiological changes on the growth of *Tecomella undulata* need to be analysed in the future.

The changes in edaphic factors due to increased irrigation and agriculture using chemical fertilisers will also impact the species distribution as it alters the soil composition by increasing the nitrogen content and cation exchange capacity. Apart from chemical fertilisers, the increase in temperature and erratic precipitation patterns will also contribute to changes in edaphic factors (Fang et al., 2017; Joseph et al., 2018), which needs to be accounted for in our study for the past and future.

The changes in landscape patterns due to urbanisation and agropastoralism also considerably impact suitable habitats. Northwestern India is one of the most highly populated drylands in the world (Sikka, 1997). Human habitation has been evident in the region since 7000 BCE (Possehl, 2002), and the region was part of the Harappan civilisation (Singh, 1971; Singh et al., 1974). The rangelands are converted to farmlands, housing plots, urban areas, and industrial areas to sustain the human population, making suitable habitats fragmented and isolated. The environmental change in the landscape leads to water bodies like lakes and rivers drying up and intensifying desertification, for example, the Saraswati River (Saini et al., 2020). The analysis of past conditions that influenced the distribution of *Tecomella undulata* is limited because of the need for fossil, geological, and archaeological records. The rate and factors influencing changes in landscape and desertification should be considered and need a thorough investigation in future research.

5. Conclusions

The global effects of climate change on ecosystems are on the rise. The predicted warming scenario predicts an expansion of dryland ecosystems and their species. The dryland ecosystems are highly unstable and fragile, so a light disruption can thwart the region's entire dynamics, making the endemic species endangered. To analyse this, we selected the Northwestern region of India and *Tecomella undulata*, a native species that can survive in harsh conditions. The species' response toward climatic variability since the LGM up to 2100 is modelled, showing that the suitable habitats are mainly located in Northwestern India, with isolated suitable habitats in Gujarat and Tamil Nadu. The results show that bio12, bio8, total nitrogen, cation exchange capacity, and bio15 are the crucial factors influencing suitable habitats. The past distribution of the species during the LGM and the middle Holocene was restricted to the arid areas of the region, and the distribution increased to the present condition, where it covers more parts of the region. The extremely suitable habitats are expected to increase by more than five times the current area under SSP5 in 2081-100 from the current level as the conditions get warm, which will suit the species' growth. The study predicts that the climatic conditions will favour the distribution of *Tecomella undulata*, whereas the edaphic factors have a mixed response.

Further studies are needed to determine how genetic, physiological, and anthropogenic factors affect the species. As the species is currently endangered, there is a need to set up more conservation sites, and our study identified Priority Conservation Areas (PCAs). A coordinated approach by researchers and policymakers could do wonders in conserving the endemic native plants in drylands.

CRedit authorship contribution statement

Jereem Thampan: Writing – original draft, Investigation, Formal analysis, Data curation. **Jyoti Srivastava:** Writing – review & editing, Visualization, Supervision, Conceptualization. **Pooja Nitin Saraf:** Methodology, Formal analysis. **Pujarini Samal:** Validation, Software.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jereem Thampan reports financial support was provided by Council of Scientific & Industrial Research. Pooja Nitin Saraf reports financial support was provided by India Ministry of Science & Technology Department of Science and Technology. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2025.105317>.

Data availability

Data will be made available on request.

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