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Ecological niche modelling of *Tecomella undulata* (Sm.) Seem: an endangered (A2a) tree species from arid and semi-arid environment imparts multiple ecosystem services

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Abstract

The objective of this study was to utilize niche modelling techniques and predictors, including bioclimatic, soil, habitat heterogeneity indices, and land-use land cover (LULC), to ascertain the present and potential distribution of *Tecomella undulata* in India. The bio-climatic variables of 2050 and 2070 timeframes were employed to forecast future occurrences. The study also examined the level of indigeneity of *T. undulata* and analysed the factors that impact its fundamental and realized niche. The Maxent model utilized for forecasting the distribution of *T. undulata* demonstrated a high level of precision, incorporating both bioclimatic and non-bioclimatic variables. The study highlights the significance of mean and maximum temperatures during the warmest quarter and month, as well as the wettest months and years' worth of precipitation. In addition, threshold values for these predictors were calculated. In contrast to the limiting effects of climatic factors, the species in question was found to exhibit a greater degree of facilitation in response to soil conditions (including rooting conditions, nutrient availability, and salt excess), habitat heterogeneity indices (such as range, maximum, and coefficient of variance of diversity), and lLULC predictors (including urban areas, residential and infrastructure development, forested regions, and sparsely vegetated areas). As a result, this species was able to expand its range across a wider expanse of India. The Churu and Jhunjhunu districts and a transact region including Pali, Jalor, Jodhpur, Sanchor, and Barmer have been identified as the best possible locations for its occurrences. Shrinkage would begin around 2050 in all of these areas. By 2070, the Churu and Jhunjhunu regions had become significantly more fragmented, while the Jodhpur region and the surrounding areas of Barmer, Sanchor, Jalor, and Vav had grown. Specific coordinates were also identified pertains to zone of extinction, zone of re-occurrence and zone of maximum occurrence. The aforementioned discoveries enable us to ascertain the extent of land that is conducive to the growth of *T. undulata* across diverse ecological niches, as well as the underlying factors and critical points that impact its dispersion dynamics both presently and prospectively. This shall aid us in determining the necessity of extensive captive cultivation for the preservation of the species and its consequential ecological advantages.

Keywords Endangered species · Habitat heterogeneity · IUCN · Land use land cover · Maxent · Percent indigeneity

Introduction

Tecomella undulata (Roxb.) Seem. (Bignoniaceae) is a deciduous or nearly evergreen ornamental tree which is highly sought after for their high value timber quality, and this monotypic genus is well-suited to arid climates (Kar et al. 2009). It has been documented from the driest parts of Arabia, southern Pakistan, and north-western India up to an elevation of 1200 m (Tewari 2007; Rezanejad and Hakemi 2017; Zolfaghari et al. 2017; Zolfaghari and Mordi 2018). Within India, a considerable population of this species can be found in western Rajasthan, where it is known as rohida, Desert teak, or 'Marwar Teak of Rajasthan, and

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is designated as the state flower of Rajasthan. Specifically, within Rajasthan, this species has been documented from districts like Barmer, Jaisalmer, Jodhpur, Pali, Jalore, Ajmer, Nagaur, Bikaner, Churu, Jhunjhunu, Rattangarh, and Sikar (Jindal et al. 1987). Other states with sparse populations have also been noted, including Maharashtra, Gujarat, Punjab, and Haryana (Bhiwani, Tosham, Ding Mandi, Jhumpa, and Balsamand).

This particular arboreal variety is widely acknowledged as a staple in the realm of arid region agroforestry, owing to its remarkable fortitude in the face of adverse environmental factors such as aridity, frigidity, fire, and dust storms. The adaptability of this particular species is noteworthy, as it has demonstrated the capacity to thrive across a diverse array of geomorphological units, including both flat and undulating terrain (Mathur and Mathur 2023). It thrives in locations with limited rainfall (150–500 mm per year) and harsh temperatures; it can endure extreme cold (0 to −2 °C) in winter and excessive heat (48–50 °C) in summer (Mohsenzadeh et al. 2012). It may grow in soil with a pH range of 6.5–8.0 with a texture ranging from loamy to sandy loam. It may grow in soil with a pH range of 6.5–8.0 with a texture ranging from loamy to sandy loam. Known for its ability to act as a windbreak and a stabilizer for eroding sand dunes in arid regions, this species also acts as a soil binder by spreading a web of lateral roots just below the surface (Kumawat et al. 2012; Tyagi and Tomar 2013). Due to its greater survival rates in water and nutrient poor soils in desert locations and extreme drought conditions, this plant is particularly useful for landscaping (Fig. 1A), blossoms and pods are loved by camel, goats, and sheep (Singh 2004) and afforestation (Fig. 1B) of drier tracts (Bhau et al. 2007). This species is essentially self-incompatible, with significant flower color variations that can be yellow (Fig. 1C, D), orange (Fig. 1E, F), and red (Fig. 1G, H), and such morphotypes may be linked with pollinator (*Pycnonotus cafer* and *Pycnonotus leucotis*) and robber (*Nectarinia asiatica*) preference (Singh

et al. 2014) as well as growing conditions, for example, orange color is more noticeable in higher stress conditions (Negi et al. 2011).

Its wood is comparable to that of teak (*Tectona grandis* L.). Because it is soft, durable, and easy to polish, it is used to manufacture engraved furniture, farming equipment, carvings, and wood is an excellent source of both fuel and charcoal (Kumar et al. 2008). *Tecomella undulata* is revered for its medicinal benefits in both modern Western medicine and more traditional indigenous medical practices. Researchers in India and Pakistan have reported on the species' pharmacological benefits (Goyal et al. 2010; Tareen et al. 2010; Dhir and Shekhawat 2012).

The precarious state of the desert teak, despite its diverse attributes and significance to impoverished communities inhabiting arid and rural regions, can be attributed to the deleterious effects of overexploitation and inadequate conservation measures (Ahmad et al. 2019; Zhang et al. 2020; Xu et al. 2021). The conventional method of seed propagation is rendered feeble owing to the diminished viability of seeds and unsuitable harvesting techniques. Furthermore, the local populace exhibits scant regard for conservation efforts. The exacerbation of the issue is brought about by the heightened frequency of interbreeding, which results in the elimination of favorable silvicultural characteristics. The modalities of vegetative reproduction of this tree, which exhibits a slow growth pattern, have yet to be comprehended by scholars (Negi et al. 2011). Efforts to propagate this arboreal species through in vitro methods have encountered several obstacles, chiefly attributable to the tree's languid growth rate, inadequate rooting capacity, and incapacity to thrive in open terrain (Kalia et al. 2014). One of the primary issues with this tree, and one of the reasons it does not grow as well as it should, is that it is susceptible to attack by wood decaying fungi and borers (Fig. 1I), leading to its death (Fig. 1J). Two species of imperfect fungi (*Phoma* sp. and *Botryodiplodia theobromae*) were found primarily responsible for

Fig. 1 *Tecomella undulata* a high valued timber species also used for arid areas' landscaping (**A**) Intact stem of *T. undulata*, source of high valued timber (**B**); three morphotypes of flower colors yellow (**C**, **D**), orange (**E**, **F**), and red (**G**, **H**); infected stem decreasing its timber quality (**I**); completely dried tree due to fungal infection (**J**)
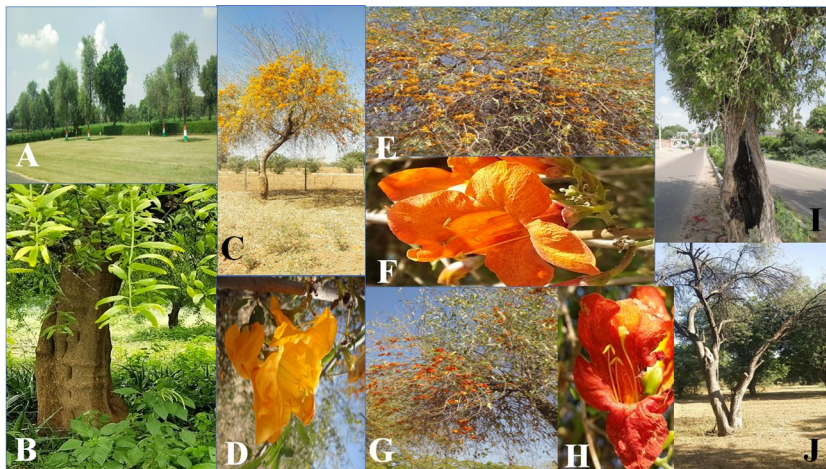
canker-rots, which subsequently attract borers and heart rot pathogen (F*omes* sp. Kalia et al. 2014).

In recent decades, the impact of climate change and other factors that contribute to extinction has significantly influenced the distribution patterns of various species (Arajo et al. 2011; Franklin 2013). The task of reinstating and safeguarding threatened species is a formidable one, primarily because of the dearth of biogeographical information pertaining to these species, as posited by Zhang et al. (2020). Consequently, novel applications of technological progressions such as machine learning, ecological theories, and geographic information systems (GIS) are being implemented in the domains of ecology and conservation (Warren et al. 2008). The utilization of species distribution models (SDMs) or ecological niche modeling enables researchers to scrutinize the correlations between abiotic factors and species occurrence data within their indigenous environment. Numerous scholars depend on SDMs to prognosticate the forthcoming ranges of flora and fauna (Ab Lah et al. 2021). Studies have shown that climate variables like temperature, precipitation, and humidity can be used to predict a species' future distribution (Smeraldo et al. 2021). The MaxEnt model represents a paradigmatic instance of a niche model that effectively merges the maximum entropy principle with a cutting-edge machine learning technique, thereby enabling the accurate forecasting of the expected ecological distributions of various species. Notwithstanding the paucity of information regarding the non-existence of a particular organism, MaxEnt managed to precisely predict the occurrence records and strata of ecological attributes grounded on the appropriateness of the habitat.

The World Protection Monitoring Centre (WCMC), Nairobi, Kenya, which is part of the United Nations Environment Programme (UNEP-WCMC and IUCN 2020), has classified *T. undulata* as a "Category 1-Indeterminate" vulnerable plant due to its current state (Kumar et al. 2008). In spite of this, a 2020 assessment by the International Union for Conservation of Nature found that *T. undulata* as Endangered according to criteria A2a (Plummer 2021). The dearth of ecological niche modelling investigations pertaining to this particular species, as evidenced by the literature, implies that the ramifications of both climatic and non-climatic factors on its distribution patterns have been significantly disregarded. Through a comprehensive analysis of these parameters, it is plausible that our knowledge can enhance our ability to predict the prospective niche dimensions and ecological aptness of this particular species in the times to come.

The current study employed information pertaining to the distribution of the *T. undulata* species for the subsequent objectives: (a) determine the current geographical distribution of this economically and ecologically important tree in India and predict the possible sites of occurrence of this species using niche modelling tools, with the help of predictors such as current climatic, soil variables, community dynamics in terms of habitat heterogeneity indices, and land-use land cover variables (b) foresee the impact of future climatic changes on the distribution of *T. undulata,* by using two climatic time-frames, 2050 and 2070 (c) to evaluate the degree of indigenous (percent indigeneity) by using the area, habitat suitability categories, and number of polygons identified in the preceding first two steps, (d) to quantify the effects of temporal climatic as well as non-bioclimatic variables on its fundamental and realized niche. The aforementioned objectives shall serve as a guiding principle in the estimation of the actual area that is conducive to the survival of the *T. undulata* across various habitat classifications. Additionally, the identification of the factors and thresholds that influence the prevailing and prospective distribution patterns of the species shall be undertaken. Consequently, it will enable us to determine the feasibility of executing comprehensive captive plantings to ensure the perpetual survival of this species and sustain the current ecological advantages it affords.

Material and methods

The dependability of anticipated outcomes is contingent upon the trustworthiness of the species' location points utilized in niche modelling, and the incidence data is predicated on approximations of probable acceptable distribution under climate change scenarios, as posited by Hefley et al. (2014). Distributional records of the *T. undulata* were collected from a variety of data repositories, including the Global Biodiversity Information Facility (GBIF 2022 https://doi.org/10.15468/dl.g2qa9n), the Indian Biodiversity Portal (https://indiabiodiversity.org/species/show/33318), published literature, and field observations (Jindal et al. 2009, 2010; Negi et al. 2011; Chhajer et al. 2018; Kumar 2018; Daneva et al. 2020). Using high-resolution Google Earth satellite image data and GIS ArcMap (Coban et al. 2020), the coordinates of these locations were determined in a WGS84 coordinate system. In addition, precise geo-coordinates were obtained by determining latitude and longitude values in Google Earth (http://ditu.google.cn/) in cases where occurrence data was not available (Xu et al. 2021). These sources yielded 168 presence points and further spatial autocorrelation and duplicate records were removed with using Spatial Thin window of the R-based Graphical User Interface Wallace Software (Kass et al. 2018) and a thinning distance of 10 kms. Following the process of spatial thinning, a total of 155 presence points were partitioned into two distinct sets of data, with 70% allocated for training and 30% for testing purposes. The distributional localities were compiled into a CSV database using the aforementioned sources (csv).

Bio-climatic (BC) and non-bioclimatic variables (NBC)

More research into the likely distribution areas of endangered plant species in terrestrial environments as a result of climate change is required for proper identification and rehabilitation efforts. Predictions of future distributions of species have been shown to be possible using machine learning techniques (Sérgio et al. 2007; Phillips and Dudik 2008; Tittensor et al. 2009; Sarikaya et al. 2018; Wei et al. 2018). The present research has employed future climate projections derived from the BCC-CSM2-MR model based on CMIP5. The Beijing Climate Center in China created this coupled climate model. In terms of tropospheric air temperature and circulation, the BCC-CSM2-MR has been shown to perform better in East Asia and the Indian monsoon region (Wu et al. 2019; Kumar and Sarthi 2021; Sun et al. 2021; Rawat et al. 2022). Maximum entropy modeling studies in the Asian region have found success with this model (Cao et al. 2021; Gao et al. 2021; Zhou et al. 2021; Arshad et al. 2022; Rawat et al. 2022).

There are four different shared socioeconomic pathways (SSPs) for climate change outlined in the sixth IPCC assessment report: SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-85 (Sohel et al. 2016; Meinshausen et al. 2020). The current study has elected to utilize the SSP2-4.5 scenario, characterized by a state of equilibrium in greenhouse gas emissions during the period of 1970–2000, and a general decrease in the global mean temperature, consequent to anthropogenic intervention. WorldClim version 1.4, which can be found online at https://worldclim.org/data/cmip6/cmip6clim30s.html, was used to derive the bioclimatic variables used to predict current and future distributions, with a spatial resolution of 30 s (1 km²) (accessed on 21st April, 2022).

The data for India was procured at a spatial resolution of 30 arc sec, which is approximately equivalent to a resolution of 1×1 km. The data was collected for the current climate as well as two future climate scenarios, namely the 2050-time frame that represents the mean values from 2041 to 2060 and 2070 that represents the mean values from 2061 to 2080. These findings have been reported by Coban et al. (2020). Subsequently, the information was truncated and transmuted into ASCII format, specifically ESRI ASCII, utilizing DIVA-GIS version 7.5, as expounded by Hijmans et al. (2001) and Zhang et al. (2021). Ahmad et al. (2019) have previously argued that the current, 2050, and 2070 years should be used for SDM analysis based on climate projections. The information regarding each bio-climatic parameter can be found in Table 1.

Soil qualities

The harmonized world soil database (HWSD) is a 30 arc-second raster database with over 15,000 different soil mapping units that combines existing regional and national updates of soil information worldwide. The HWSD is composed of a GIS raster image file linked to an attribute database in Microsoft Access format. For the present work, six soil quality properties like nutrient availability, nutrient retention capacity, rooting conditions, oxygen availability

Table 1 Description of predictive bio-climatic variables use in this study (downloaded from WorldClim related to four time-frames: current, 2050 and 2070 of Shared Socioeconomic Pathways (SSPs 4.5 scenario)

Code	Environmental variables and their abbreviations	Scaling factor	Unit
BC-1	Annual mean temperature (AMT)	10	°C
BC-2	Mean diurnal range (MeDR)	10	°C
BC-3	Isothermality (BC2/BC7) ($\times$100) (Iso)	100	–
BC-4	Temperature seasonality (standard deviation $\times$ 100) (TempS)	100	–
BC-5	Maximum temperature of warmest month (MaTWaM)	10	°C
BC-6	Minimum temperature of coldest month (MiTCM)	10	°C
BC-7	Temperature annual range (BC 5–BC 6) (TAR)	10	°C
BC-8	Mean temperature of wettest quarter (MeTWeQ)	10	°C
BC-9	Mean temperature of driest quarter (MeTDQ)	10	°C
BC-10	Mean temperature of warmest quarter (MeTWaQ)	10	°C
BC-11	Mean temperature of coldest quarter (MeTCQ)	10	°C
BC-12	Annual precipitation (AnPr)	1	mm
BC-13	Precipitation of wettest month (PrWeM)	1	mm
BC-14	Precipitation of driest month (PrDM)	100	mm
BC-15	Precipitation seasonality (coefficient of variation) (PrS)	1	Fraction
BC-16	Precipitation of wettest quarter (PrWeQ)	1	mm
BC-17	Precipitation of driest quarter (PrDQ)	1	mm
BC-18	Precipitation of warmest quarter (PrWaQ)	1	mm
BC-19	Precipitation of coldest quarter (PrCQ)	1	mm

to root, excess salt and toxicity. Details characteristics of these were provided by Fischer et al. (2008). In this study, the advice of Zhao et al. (2021) has been followed, who stated that parameters related to landcover, soil, and HHI are unlikely to change significantly in the near future.

Habitat heterogeneity index

According to niche theory, a greater degree of diversity is associated with a more diverse ecosystem. This is because, through niche partitioning, more species may be able to coexist in a given area if that area is more heterogeneous. Tuanmu and Jetz (2015) developed 14 metrics to describe the diversity of habitats all over the world at a resolution of 1 km. These metrics were derived from the texture of enhanced vegetation index (EVI) images obtained from the moderate resolution imaging spectroradiometer (MODIS). Six first-order and 8 s-order texture measures are accessible (http://www.earthenv.org/texture) at 30 arc-second (~ 1 km at the equator), 2.5 arc-minute (~ 5 km) and 12.5 arc-minute (~ 25 km) resolutions. In the scope of our research, a dataset comprising of 30 arc seconds was employed, with a particular focus on first-order texture measures (coefficient of variation = normalized dispersion of EVI; evenness = evenness of EVI; range = range of EVI; Shannon and Simpson indices = diversity of EVI; standard deviation = dispersion of EVI) and to second order texture measures (uniformity = orderliness of EVI; maximum = dominance of EVI combinations).

Land use and land cover (LULC)

Different LULC predictor namely rain-fed and irrigated cultivated land, total cultivated land, forest, grass/scrub/woodland (GRS), barren/very sparsely vegetated land (NVG), urban land and land used for housing and infrastructure and water bodies are utilized for ENM of this species. These variables were downloaded from https://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/ and utilized as recommended by Fischer et al. (2008)

Data processing

Issue of multicollinearity

By comparing the cross-correlation to the Pearson correlation coefficient (r), the multicollinearity test was used to lessen the possibility of over-fitting in the current investigation. In addition, variables with a high cross-correlation coefficient (greater than 0.85) were eliminated one by one (Pradhan 2016). These results were derived using the Niche

Tool Box (Osorio-Olivera et al. 2020; https://github.com/luismurao/ntbox).

In order to address the concern of multi-collinearity among predictor variables, the methodologies proposed by Kumar et al. (2006) were employed. Because of its biological relevance to the species and its ease of use in model interpretation, one of two strongly correlated variables was selected (Kumar and Stohlgren 2009; Padalia et al. 2014). As a result, each group of variables with a high $r^2 > 0.85$ of correlation or higher was reduced to a single, remaining variable (Ma and Sun 2018). To train the model, 70% of the data was used, while 30% was used for testing (Mousazade et al. 2019).

Projection assignment and their transformations

Prior to extracting data and generating predictions through the utilization of the machine learning model, it is imperative to rectify the estimations of both the bio-climatic (BC) and non-BC variables. These variables were procured from disparate sources and at varying resolutions. Our analytical approach involved adhering to a prescribed methodology within ArcMap, with the assistance of ArcToolbox. The delineation of the projection was initially expounded upon in the "projection and transformation" section of the Data Management Tools interface. The World Geodetic System 1984 EASE geographic coordinate system (GCS) was employed for this purpose. Subsequently, the habitat class raster file's projections were converted to WGS 1984 web Mercator (auxiliary sphere-3857) with the intention of utilizing the "calculate geometry" window of Arc Map to assess the area encompassed by each habitat suitability class (as depicted below). In order to advance, let us assume that our objective is to ascertain the area encompassed by a particular category, employing a metric of the user's preference (in our case, square kilometers were utilized).

Species distribution modelling

In this study, the Maxent 3.4.1 software (http://www.cs.princeton.edu/schapire/Maxent/) was used to simulate and predict the potential geographical distribution probability of *T. undulata* under current and two futures (2050- and 2070-time frame) scenarios as well as three non-climatic variables as mentioned above. By employing this tool to each predictor independently, one can precisely gauge their respective influence on the distributional pattern of the species. During the modelling process, 70% of the 155 *T. undulata* distribution data samples were randomly selected as training data, while 30% were used as testing data. The number of background points generated at random was set to 10,000 (Zhang et al. 2021). In order to mitigate the issue of over-fitting in the test data, the present study opted to

set the regularization multiplier at 0.1 (Phillips et al. 2006). The utilization of linear, quadratic, and hinge properties was implemented. The Jackknife method was employed in the environment parameter configuration, while the remaining parameter settings were kept at their respective software defaults. To calibrate and validate the robustness of Maxent model evaluation, threshold-independent receiver-operating characteristic (ROC) analyses were used, and an area under the receiver operating curve (AUC) was used to estimate the accuracy of the model predictions (Elith et al. 2006). The performance of the model was classified as failing (0.5–0.6), poor (0.6–0.7), fair (0.7–0.8), good (0.8–0.9), or excellent (0.9–1.0). AUC values close to one indicate that the model is doing well (Araujo et al. 2005).

The permutation importance (PI) value and response curves were utilized to evaluate the effects of bio-climatic and non-bioclimatic variables on the distribution of this species (Mishra et al. 2021; Mathur and Mathur 2023). Then used ArcGIS to convert the Maxent output ASCII file into raster format and used this to categorize the habitat areas as optimal (1.0–0.80), moderate (0.80–0.60), marginal (0.60–0.40), low (0.40 and 0.20), and absent (> 0.20). Subsequently, the most optimum raster file underwent a conversion process to keyhole markup language (KML) format, thereby enabling the identification of exact coordinates of optimal habitats. Each raster file was then converted to XYZ format so that the Kernal density (PAST software; Hammer et al. 2001) could be calculated, revealing the coordinates of optimal sites across India and allowing us to identify the zone of extinction and zone of highest occurrence.

Niche overlap

Recent research into niche overlap has compared and predicted actual patterns of suitability ratings across space and time. Niche overlap between two studied parameters was quantified using the Maxent ASCII output of each analysis. To achieve this, ENMTools was employed (Warren et al. 2010). The analysis's stated goal was to provide a visual representation of the predicted area retained by this species. *Schoener's D* (which measures the uniformity of niche overlap per pair) and *Hellinger's-based I* (which measures the degree of overlap of the geographical distribution) were utilized to represent the ecological niche overlap. D and I values were between zero and one. These overlaps in *I* and *D* are determined by subtracting the species' suitability scores at each grid cell, after suitability has been standardized to add up to 1 across the entire area of interest (Karami et al. 2020). The value increase would help ecological niches overlap more effectively (Ahmad et al. 2019).

Ellipsoid niche hypervolume

In order to better predict where this species might be found, models based on machine learning provide a number of important variables. Hypervolumes of species' niches were measured using the top three predictors across all bioclimatic scenarios and three studied non-bioclimatic predictors. In the course of this study, NicheToolBox software (Ntbox Osorio-Olivera et al. 2020) was Ntbox, a GUI tool written in the R programming language, calls for the raster output of BC variables. By calculating the species' environmental values' centroid and covariance matrix, ellipsoidal models were constructed. It goes from the geographical centre outward to all possible settings in the research region. By employing this approach, it is feasible to ascertain the environmental determinants that govern the fundamental and realized niche of the organism in question.

Automated conservation assessments (AA): I and II

Using the R program "*ConR,*" extent of occurrence (EOO Sq km), area of occupancy (AOO Sq km), number of unique occurrences, number of subpopulations, number of locations, IUCN (2021) threat category according to Criterion B, and IUCN annotation (category code) were calculated (Dauby et al. 2017; Kass et al. 2021). ArcMap output of Maxent analysis with different predictors was transformed into a "XYZ" file format which further convert into "CSV" format for *ConR* program. Since above files are output of ENM analysis, overfitting was a concern, therefore, our approach in ConR involved limiting the selection of coordinates for EOO and AOO estimation to those that satisfied all optimal habitat suitability criteria. Adhikari et al. (2018) and Marco et al. (2018) argued for similar methods.

Percent indigeneity

Percent indigeneity (PI) using a newly proposed index in which the habitat suitability classes were weighted as follows:

Per cent of Indigenous

$$= \frac{\text{Habitat suitability type} \times \sum_{i=0}^{n} polygon\, number}{\sum_{i=0}^{n} Area\,(sq.\,km)} \times 100$$

Habitat suitability type scoring factors = optimum = 1; Moderate = 0.75; Marginal = 0.50 and Low = 0.25. $\sum_{i=0}^{n} polygon\, number$ = sum of polygon numbers pertains to a specific suitability class and $\sum_{i=0}^{n} Area\,(sq.\,km)$, represent the total area (sq. km) occupied by the species under the specific suitability class. High index value represent higher probability to generality and lesser value represents the restriction of this species within the confined zone.

Results

Based on multicollinearity test, BC 1, 2, 4, and 19 were eliminated from SDM model preparation with all three climatic time frames (current, 2050, and 2070 Table 2). Similarly, the symbol "x" in Table 2 denotes other variables excluded from this study for the same reason. In addition, all three climatic time frames were used with BC-3, 5 and 6. BC7 and 15 were used with current and 2070; BC-8 and 18 with 2050 and 2070; and BC9, BC-10, and 12 with current and 2050. While BC 11 and 13 were specifically used with current and 2070 scenarios, respectively. Similarly, BC14, 16, and 17 were exclusively utilized for model preparation with 2050 only (Table 2). Similarly, nutrient retention capacity and oxygen availability to root variables of soil parameters were excluded as these non-climatic variables had significant multi-collinearity with others. Simpson Indices were excluded from the HHI. There was no such significant correlation found between the variables of LULC (Table 3).

Model performances

The area under the receiver operating curve (AUC) was used to assess the performance of the MaxEnt model for species distribution prediction. This empirical research has revealed that the machine learning tool in question exhibits exceptional performance, as evidenced by its AUC score surpassing 0.97 across all three bio-climatic temporal frame (Fig. 2a current; b 2050 and c 2070) and for soil and LULC with AUC more than 0.95; Fig. 2d, f, respectively. However, our model quality was good (AUC > 0.84) with HHI predictor (Fig. 2e).

Tables 2 and 3 illustrates and permutation importance (PI) scores of the bio-climatic variables with their over three climatic timeframes and non-climatic variables (soil, HHI and LULC), respectively. Percent contribution values are only intuitively defined; they are based on the specific path taken by the Maxent code to arrive at the optimal solution; a different algorithm could arrive at the same solution via a different path, resulting in different percent contribution values. The second way in which a variable's significance is measured is through its permutation importance. This metric is independent of the method used to arrive at the Maxent model. The relative importance of each contributing variable is calculated by randomly switching it around in the training set (both presence and background points) and observing the impact on the area under the curve (AUC) for the training set as a whole. A large decrease indicates that the model is heavily reliant on that variable, as suggested by Phillips et al.

Table 2 Maxent output showing variables contributions to the model in form of permutation importance (PI) with respect to bioclimatic variables

Bio-climatic variables	Current	2050 RCP4.5	2070 RCP4.5
BC3 (Iso)	2.7	0.5	1.5
BC5 (MaTWaM)	37.5	0.1	48.7
BC6 (MiTCM)	2	0.4	3.5
BC7 (TAR)	0.9	x	1.4
BC8 (MeTWeQ)	x	6.2	5
BC9 (MeTDQ)	0.2	1.1	x
BC10 (MeTWaQ)	0.2	43.5	x
BC11 (MeTCQ)	0.5	x	x
BC12 (AnPr)	51.2	29.3	x
BC13 (PrWeM)	x	x	22.4
BC14 (PrDM)	x	4.8	x
BC15 (PrS)	4.7	x	14.8
BC16 (PrWeQ)	x	10	x
BC17 (PrDQ)	x	4	x
BC18 (PrWaQ)	x	0.2	2.6

Symbol x indicated the eliminated predictors due to their significant correlation with others

Table 3 Maxent output showing variables contributions of non-bioclimatic variables to the model in form of permutation importance (PI) with respect to non-bioclimatic variables

| Soil	PI	HHI	PI	LULC	PI
Rooting conditions	38	Range	41.9	Urban land and land used for housing and infra-structure	37.8
Nutrient availability	34.2	Maximum	23.7	Forest	36.1
Excess salt	21	Coefficient of variance	23	Barren/very sparsely vegetated land (NVG)	17.7
Workability	6.7	Evenness	2.7	Grass/scrub/woodland (GRS)	3.3
Toxicity	0.1	Standard deviation	7.4	Cultivated irrigated	2.2
		Shannon Index	1.2	Cultivated total	1.3
–	–	–	–	Cultivated rainfed	1.2
–	–	–	–	Water bodies	0.5

HHI habitat heterogenity indices, *LULC* land use and land cover

Fig. 2 The area under the receiver operating curve with bio-climatic time-frames (current **a**; 2050 **b** and 2070 **c**), soil (**d**), habitat heterogeneity indices (**e**) and LULC (**f**)
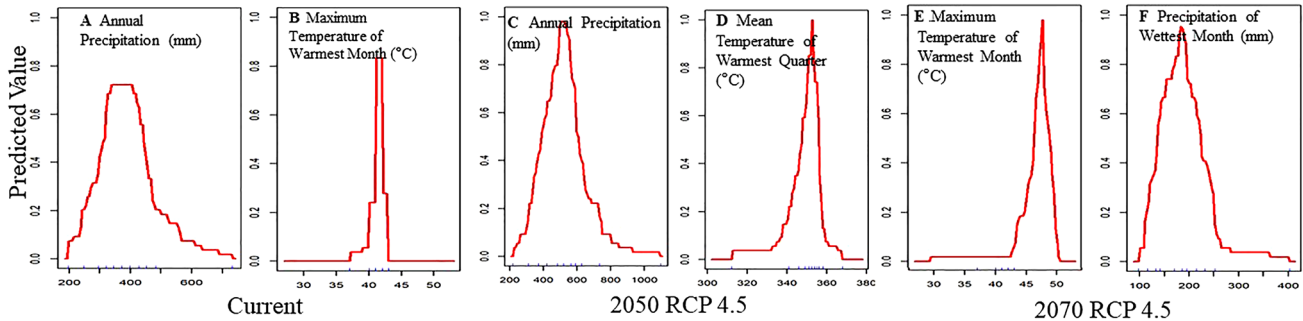
Fig. 3 Response curves with most important two climatic variables under the current (**A**, **B**; 2050 RCP 4.5 **C** and **D** and 2070 RCP 4.5 **E** and **F** conditions)

(2006) and Phillips and Dudik (2008). Current findings were consolidated by means of permutation importance, taking into account the aforementioned facts.

Annual precipitation and maximum temperature of warmest month were the most important predictors under current bio-climatic conditions, with permutation importance (PI) values of 51.2 and 37.5, respectively (Table 2). Interestingly, with a 2050 RCP of 4.5, the mean temperature of the warmest quarter (43.5 PI) and annual precipitation (PI 29.3) were the most influential variables. Additionally, current findings indicate that the maximum temperature of the warmest month (PI = 48.7) and precipitation of the wettest

month (PI = 22.4) had a significant impact on 2070 RCP 4.5. Such patterns suggested that both energy and water-related variables were important for *T. undulata*. Precipitation seasonality was identified as the third most important variable with PIs of 4.7 and 14.8, respectively, for current and 2070. During 2050 RCP 4.5, the wettest quarter's precipitation was the third most significant variable (PI = 10).

Figures 3 and 4 depicts the changes in *T. undulata* occurrence probability values as a function of key climatic, soil, community and land use variables. As mentioned above, annual precipitation played a significant role in the habitat suitability of this species under present
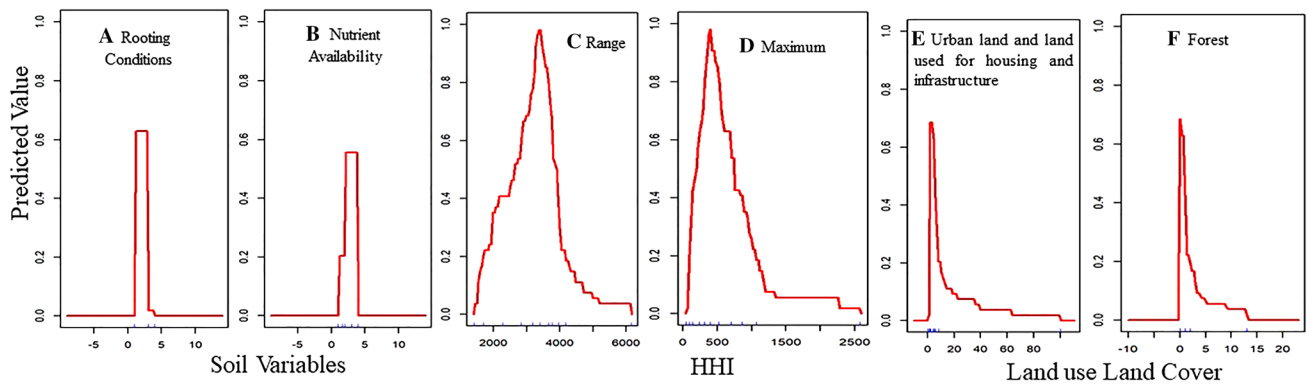
Fig. 4 Response curves with most important two non-climatic variables namely soil (**A**, **B**); habitat heterogeneity (**C**, **D**) and LULC (**E**, **F**)

and 2050 conditions; with this variable, the peak suitability was found around 300–500 mm (Fig. 3A) under present climatic conditions, and this range shifted up to the 400–600 mm (Fig. 3C) with the letter period. Also potentially influencing this species' suitability in the present and future climate (2070) is the warmest month's maximum temperature, which is most encouraging between 40 and 43 °C (Fig. 3B) and rises to between 45 and 50 °C with the letter period (Fig. 3E). Because of their limited operational window, mean temperatures for the warmest quarter; 34–36 °C during 2050 (Fig. 3D) and the precipitation of wettest month 120–250 mm during 2070 (Fig. 3F) are somewhat more constrained for *T. undulata*.

Non-bioclimatic conditions resulted in a smaller peak value for the probability of this species, in particular with soil variables such as rooting conditions (Fig. 4A) and nutrient availability to root (Fig. 4B). Peak probabilities were found to be highest for HHI variables like range (Fig. 4C, which have spectrum in between 2000 and 4000) and highest for maximum variables (40–750) (Fig. 4D). Figure 4E shows how urban and residential land use, as well as forest cover, are the most important determinants of peak probability values of 5–10 (Fig. 4E) and 1–3 (Fig. 4F), respectively.

Suitable areas of *T. undulata* under climatic and non-climatic predictors

Distribution of this species under optimum, moderate, marginal and low-quality habitats is depicted in Fig. 5 (bioclimatic) and Fig. 6 (non-bioclimatic). Table 4 shows the area (square kilometers) and number of polygons (NoPs) for these suitability classes. According to our findings, soil variables accounted for the largest optimal area (235,670 sq. km.), while HHI variables revealed the largest areas of moderate (195,304.5 sq. km.), marginal (410,387.1 sq. km.), and low (873,100.6 sq. km.) habitat types. The optimum category had the smallest area (34,278.3 sq. km.) with 2050 RCP 4.5.

Soil variables showed the smallest areas for moderate habitats (26,843.39 sq. km.) and marginal habitats (20,323.03 sq. km.). Number of polygons (NoP) representing optimal area decreases with 2050 (3) and 2070 (6) future scenario compared to present climatic conditions (12). However, NoPs under moderate and marginal habitats were generally consistent across all climatic periods (Table 4). Non-climatic variables, including LULC, HHI, and soil, rank in order of highest NoPs across all four habitat types, with the exception of optimum habitat, where soil variables rank higher in NoPs (108) than HHI (75).

The aforementioned findings indicate a notable alteration in spatial paternity. Consequently, use of KML files to expound upon our findings in relation to the most optimal habitats. The Churu and Jhunjhunu districts, the Magrasar and Rotoo (Nagor regions), the transact region spanning Pali, Jalor, Jodhpur, Sanchor, and Barmer, are among the optimum places in Rajasthan for *T. undulata* to thrive in the current climate. Optimal habitats are also located in Gujarat, close to the Tharad, Vav, and Dhima of Banaskantha district (Fig. 5a). Across all of these geographic areas, a notable reduction in size is projected to commence around 2050. This decline was most pronounced in the districts of Churu, Jhunjhunu, and Jodhpur (Fig. 5b). The Churu and Jhunjhunu regions experienced significant fragmentation by the year 2070, while the Jodhpur and Barmer, Sanchor, Jalor, and Vav areas experienced expansion (Fig. 5c). Then overlaying KML files pertaining to distinct climatic temporal zones, in order to enhance our visualization of the temporal fluctuations occurring within the optimal habitat categories; the resulting Fig. 7a, shows that the optimal habitat for this species occupies a narrow transect belt stretching from the northernmost to the westernmost parts of Rajasthan.

The state of Rajasthan as a whole, according to the *T. undulata* SDM analysis, has a favorable combination of soil variables that make up its ideal habitat (Fig. 6a). HHI provides similar optimal habitats *T. undulata* across nearly all of Rajasthan, with some more moderate and marginal types
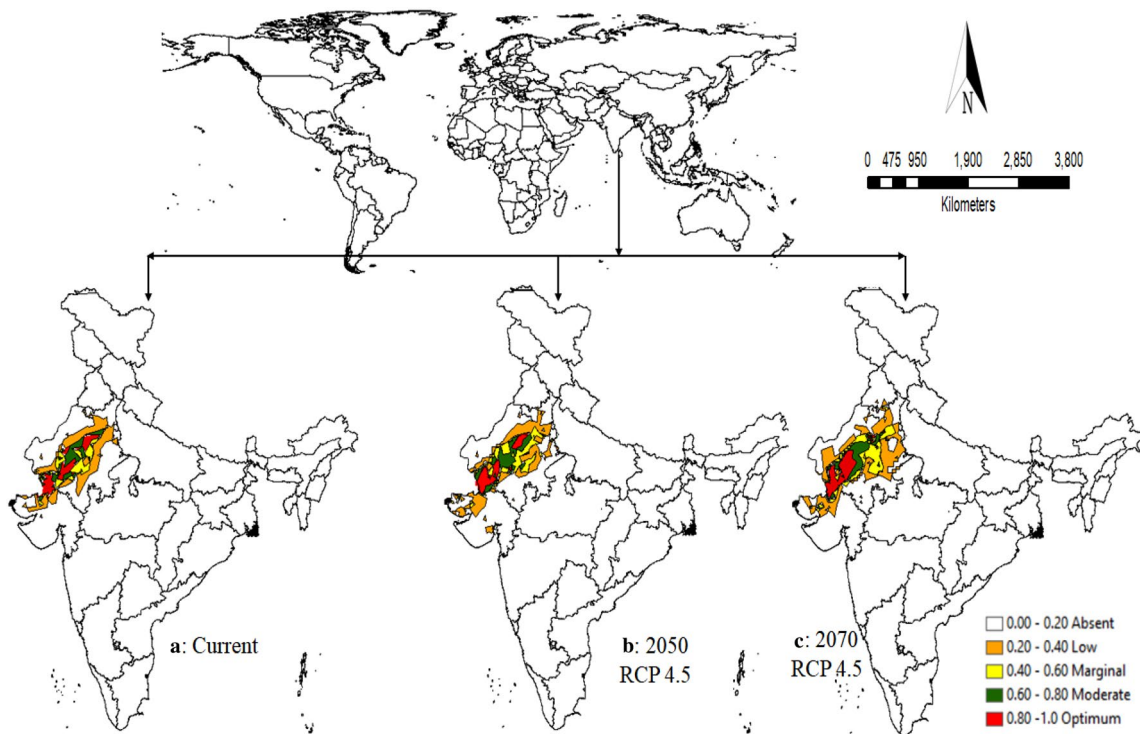
Fig. 5 Habitat suitability of *T. undulata* under different classess (current—**a**; 2050—**b** and 2070 **c**)
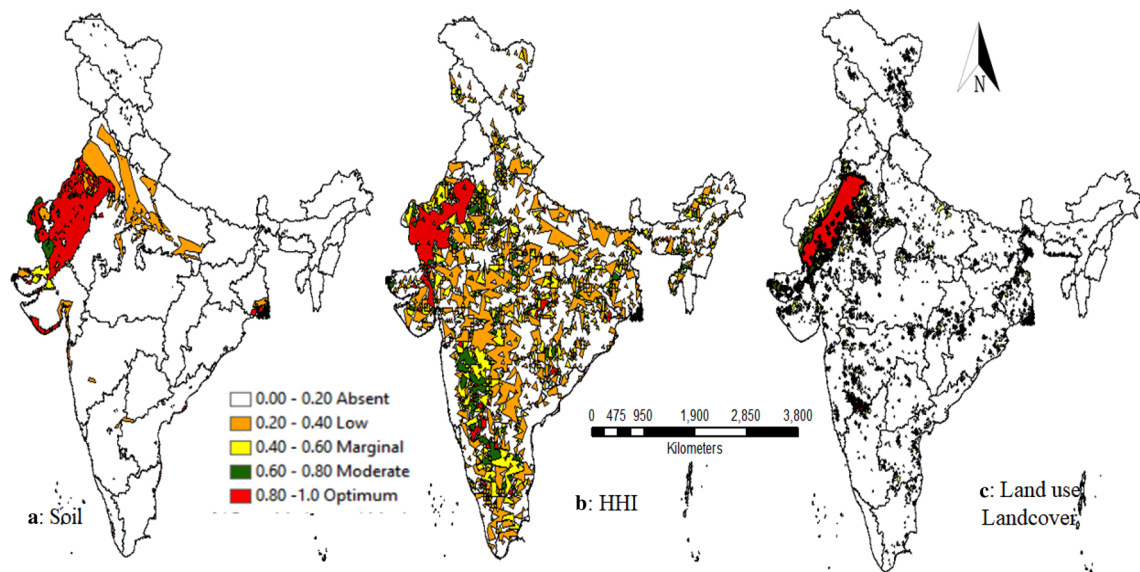
Fig. 6 Habitat suitability of *T. undulata* under different classess with soil (**a**) and HHI (**b**) and LULC (**c**)

interspersed throughout. Interestingly, the moderate, marginal, and low habitat types found in isolated pockets across much of India are also supported by these non-climatic diversity parameters (Fig. 6b). LULC data also showed a long, continuous belt stretching from the state of Rajasthan to the state of Gujarat, including the regions of Tharad, Vav,

Rapar, Bhachau, Lakhpat, Bhuj, and Khambhalia as well as the districts of Churu, Jhunjhunu, Sikar, Jalor, Jodhpur, Nagor, Pali, Barmer, and Sirohi (Fig. 6c). When these soil, diversity, and land use variables are superimposed on one another, it is easier to understand the optimal habitat for *T.*

Table 4 Area (sq. km) and number of polygons (NoPs)

Variables	Optimum		Moderate		Marginal		Low	
	Area	NoPs	Area	NoPs	Area	NoPs	Area	NoPs
Current BC	37,828.1	12	36,927.85	25	42,047.31	29	120,501.3	26
2050 RCP4.5	34,278.3	3	45,400.58	20	52,219.14	31	119,408.5	41
2070 RCP4.5	46,159.1	6	39,057.84	25	64,103.25	35	149,146.1	30
Soil	235,670	108	26,843.39	113	20,323.03	53	227,677.8	192
HHI	197,283.8	75	195,304.50	232	410,387.10	413	873,100.6	478
LULC	160,153.2	344	70,825.07	593	128,596	1033	268,842.3	1804

HHI habitat heterogenity indices, *LULC* land use and land cover
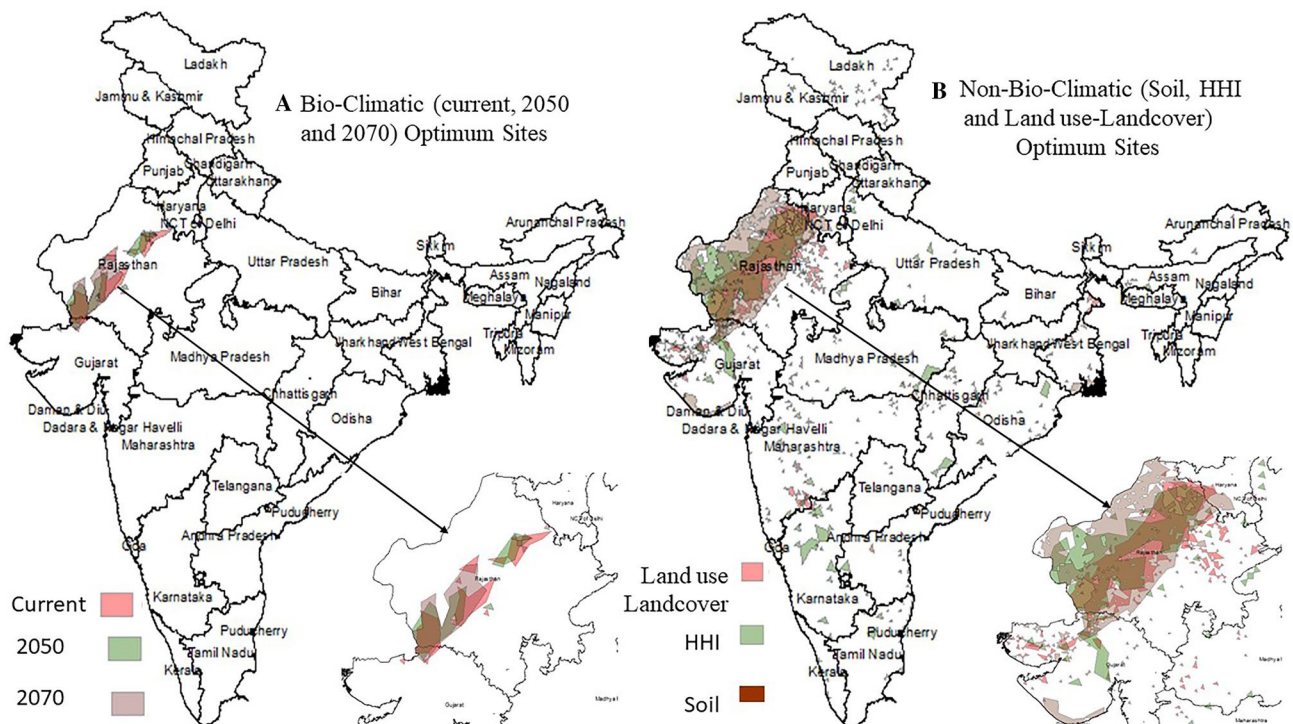

Fig. 7 Superimposition of optimum suitability sites with current bio-climatic and non-bioclimatic predictors

*undulata* because each of these factors helps to maintain distinct zoning (Fig. 7b).

This species' distribution patterns with the studied predictors can be determined using kernel density estimation (Figs. 8, 9), which incorporates the coordinates of optimal habitats. Based on our empirical observations, it appears that under the prevailing bio-climatic circumstances, the implementation of bio-climatic parameters could effectively discern the areas of extinction and resurgence in the years 2050 and 2070. Our findings indicate that, given the extant bio-climatic conditions, the species in question exhibits optimal suitability within a longitudinally extended transverse band spanning the regions of Rajasthan and Gujarat with a latitude of 24°25′ to 28°25′ to 70°50′ to 75°50′ longitude

(Fig. 8) with some intermingled other habitat types. With 2050, our result indicates zone of extinction having coordinates between 27°0′ to 27°5′ latitude and 73°0′ to 73°8′ longitude. Such extinction zone also recorded with 2070 ranging from 27°25′ to 28°0′ latitude and 73°50′ to 74°50′ longitude. Furthermore, two discrete areas of recurrences were documented with 2070 that lies between 25°25′ to 25°50′ latitude and 71°25′ to 71°50′ longitude and 26°0′ to 26°50′ latitude and 73°50′ to 74°50′ longitude. Such results are corroborated with our calculated areas (Sq.km).

With three non-climatic predictors, we identified zone of highest occurencess (Fig. 9) that lies between 23°0′ to 29°50′ latitude and 70°5′ to 76°5′ longitude with soil. $22^05′$ to $25^05′$ latitude and 70°5′ to 76°5′ longitude and $31^05′$ to $34^05′$
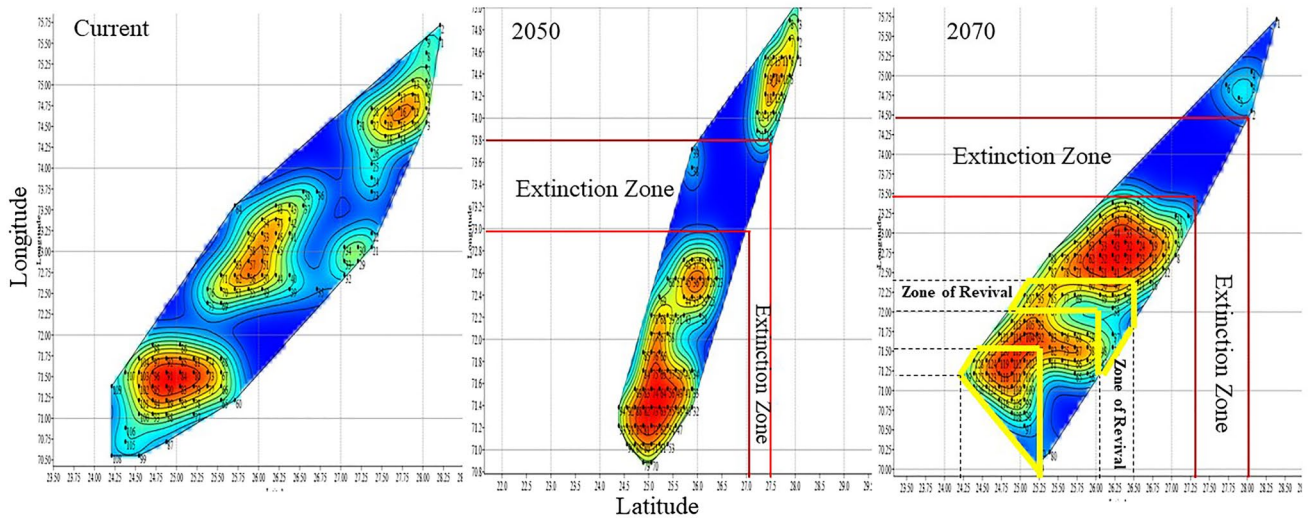
Fig. 8 Kernel density estimation of optimum suitability sites with three bio-climatic timeframes
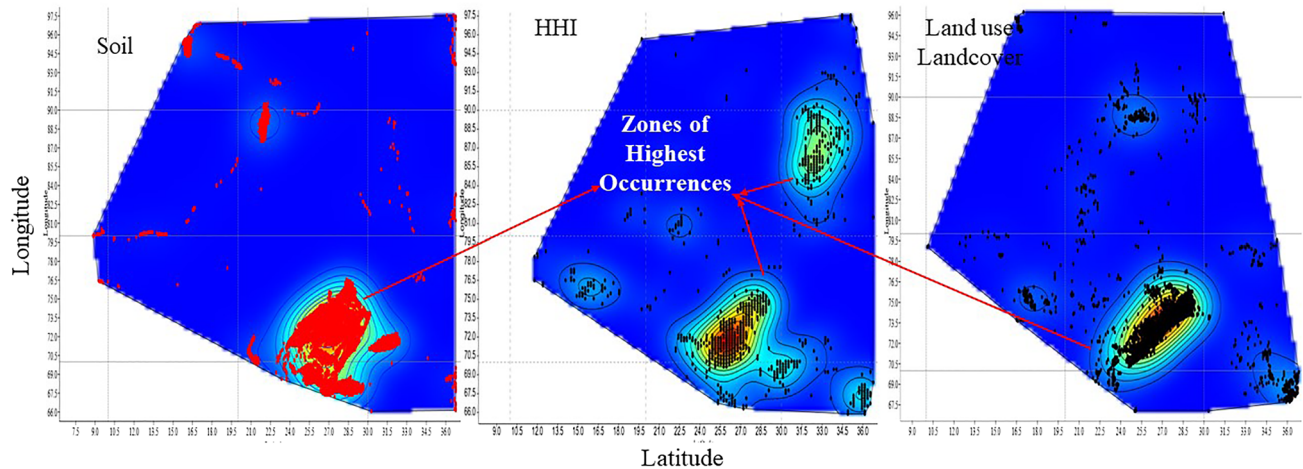
Fig. 9 Kernel density estimation of optimum suitability sites with three non-bio-climatic predictors

latitude and 84°0′ to 90°0′ longitude with HHI. With LULC such zone of highest occurrence is recorded in between 22°5′ to 29°5′ latitude and 70°0′ to 76°5′ longitude. With these predictors, there are several small patches were also noticed.

Niche overlap

The results of niche overlap (*Schoener's D*, which quantifies the stability of niche overlap per pair) and geographical distribution overlap (*Hellinger's-based I*) are shown in Table 5. The values varied from 0 to 1, with higher numbers indicating more ecological niches were shared. Non-climatic predictors had lower niche overlap (both *D* and *I*) than climatic predictors, according to our findings. Both indices had their highest values between predictor

categories, such as between climatic time frames with each other and similarly for non-climatic variables. In this context, the values of D and I between climatic variables ranged from 0.74 to 0.77 and 0.93 to 0.95, while those between non-climatic variables fell into the ranges of 0.35 to 0.50 and 0.47 to 0.66, respectively. Soil predictors had the lowest values for both of these indices in all three climatic projections (*D*: 0.29, 0.32 and 0.34 and *I*: 0.49, 0.50 and 0.57).

Ellipsoid niche hypervolume

With current dataset, ellipsoid hypervolume (multidimensional space of resources available for a species) was developed to simulate the species' fundamental niche (defined

Table 5 Niche overlap (*Schoener's D* and *Hellinger's-based I*) between two predictors

Variables	Soil	2050 RCP 4.5	2070 RCP 4.5	Current BC	HHI
Niche overlap D output					
2050 RCP 4.5	0.32	–	–	–	–
2070 RCP 4.5	0.34	0.77	–	–	–
Current	0.29	0.77	0.74	–	–
HHI	0.47	0.32	0.35	0.3	–
LULC	0.35	0.29	0.31	0.27	0.5
Niche overlap I output					
2050 RCP 4.5	0.5	–	–	–	–
2070 RCP 4.5	0.57	0.95	–	–	–
Current BC	0.49	0.95	0.93	–	–
HHI	0.65	0.56	0.61	0.55	–
LULC	0.58	0.47	0.51	0.43	0.66

as a species' ability to persist and reproduce in a broader range of environments when not competing with other species; Franklin 2013) and its realized niche (when it is in the presence of other interacting species) using projected occurrence records of *T. undulata* and the most important environmental variables identified from Maxent in form of raster output. This allows us to identify the factors that governs its fundamental and realized niche. The results are displayed in Fig. 10 (bio-climatic time frames) and Fig. 11
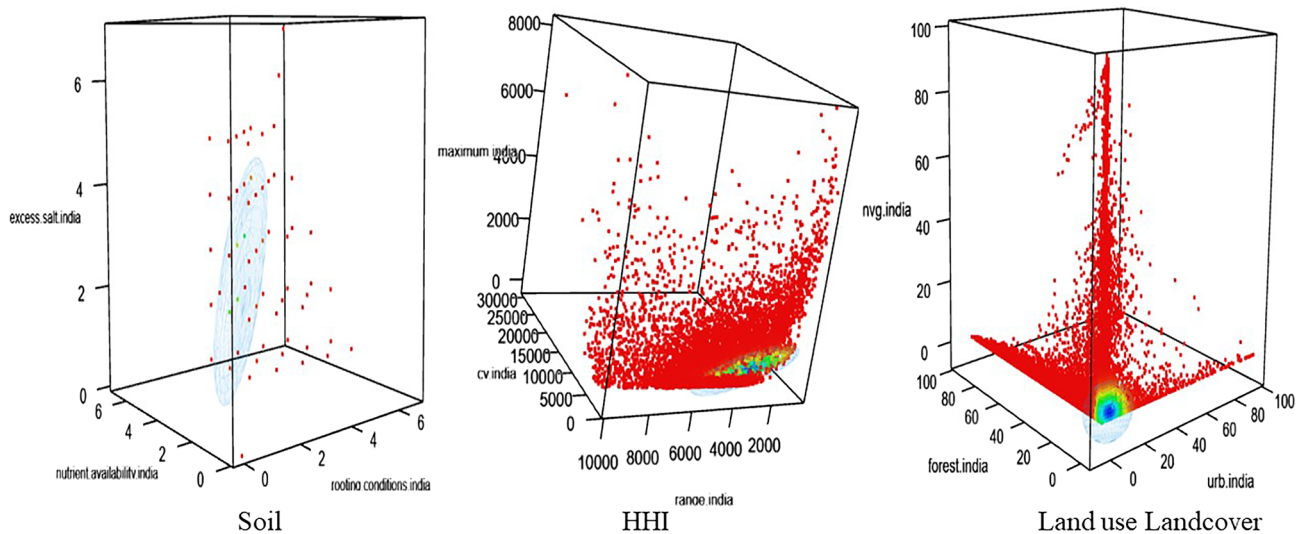
(soil, HHI, LULC). In both, the blue colour represents niche stability, the green colour represents niche unfilling (the proportion of the native niche that does not overlap with the exotic niche), and the red colour represents niche expansion (Mathur and Mathur 2023). The size of these zones corresponds to the volume of their niche. In terms of bioclimatic space, *T. undulata* ellipsoidal niche had a larger hypervolume (13.21×10^2 °C mm^2) during 2070, followed by current (50.49×10^1 °C mm^2), and was the smallest during the 2050 RCP 6.0 (11.51×10^2 °C mm^2). Among other types of predictors, largest hypervolume (46.91×10^6 °C mm^2) was identified with HHI followed with soil (14.34×10^3 mm^2) and LULC (20.01×10^2 °C mm^2).

The influence of environmental variables on niche dynamics is indicated by their centroid values. Their proximity to the centroid indicates that they exert control over species suitability (Nunez-Penichet et al. 2021). Values of centroid as well as range of different bio-climatic variables pertain three time-frames as well as non-bioclimatic variables are presented in Tables 6 and 7, respectively. Under current climatic conditions, this species has been found to show the greatest niche expansion from its fundamental niche with annual precipitation (BC-12, i.e., water variable), while precipitation seasonality (BC-15, water availability) and maximum temperature of the warmest month (BC-5) have been identified as facilitators to maintain these fundamental niche areas. Under 2050 climatic conditions, annual precipitation with a centroid value of 498.36 will continue to be as important to this species as it is under current conditions. While the precipitation of wettest quarter (BC-16) and the mean temperature of warmest quarter will help it to

a: Current BC **b: 2050 RCP 4.5** **c: 2070 RCP 4.5**
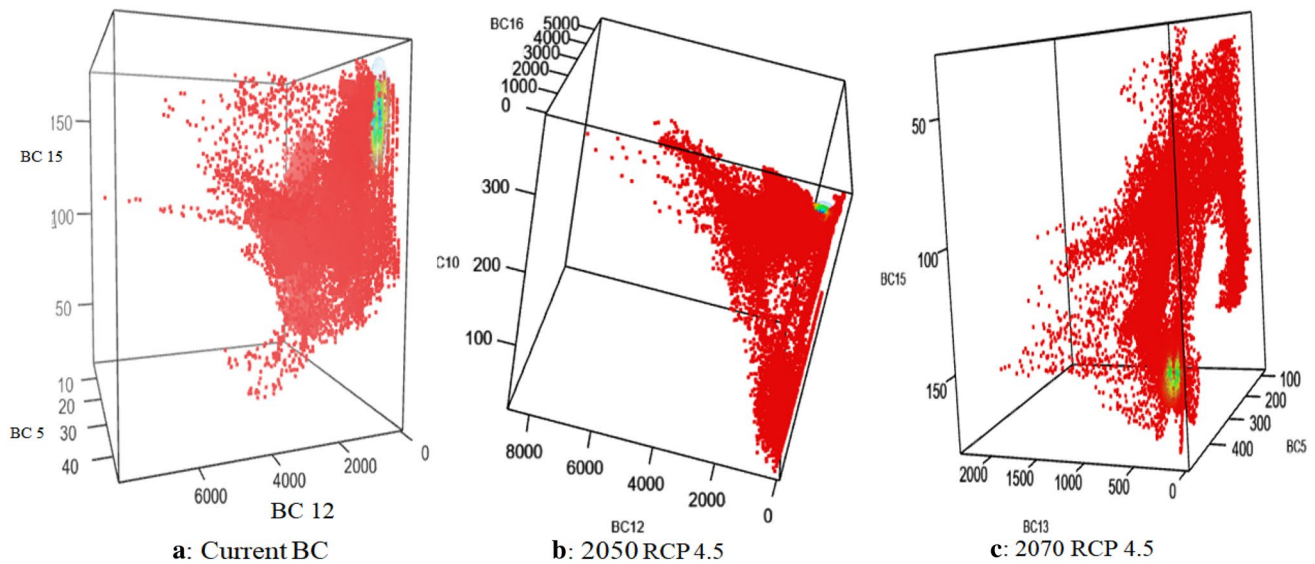
Fig. 10 Graphical representation of *T. undulata* niche hypervolume with three most influential bioclimatic variables pertains to current and 2050 and 2070 (RCP 4.5) bioclimatic time-frame. The blue colour represents niche stability, the green colour represents niche unfilling (the proportion of the native niche that does not overlap with the exotic niche), and the red colour represents niche expansion

Fig. 11 Graphical representation of *T. undulata* niche hypervolume with three most influential variables pertains to soil, habitat heterogeneity indices (diversity) and LULC variables. The blue colour represents niche stability, the green colour represents niche unfilling (the proportion of the native niche that does not overlap with the exotic niche), and the red colour represents niche expansion

Table 6 Values of centroid (and range) of three most influential bio-climatic variables pertains to various time-frames

Variable names	Current BC	2050 RCP 4.5	2070 RCP 4.5
BC-5	41.64 (40–43 °C)	–	448.85 (45–50 °C)
BC-10	–	351.67 (34–36 °)	–
BC-12	366.79 (300–500 mm)	498.36 (400–600 mm)	–
BC-13	–	–	181.87 (120–250 mm)
BC-15	147.97 (140–160%)	–	150.67 (145–155%)
BC-16	–	429.36 (300–700 mm)	–

Table 7 Values of centroid (and range) of three most influential non-bioclimatic variables pertains to soil, habitat heterogeneity indices (HHI) and land use land cover

Variable names	Soil	HHI	LULC
Rooting conditions	2.55 (2–4)	–	–
Nutrient availability	2.16 (2–4)	–	–
Excess salt	2.98 (2–4)	–	–
Range	–	3230.08 (2000–4000)	–
Maximum	–	452.80 (40–750)	–
Coefficient of variance	–	1704.60 (1000–2500)	–
Urban land and land used for housing and infrastructure	–	–	3.90 (5–10)
Forest	–	–	0.65 (1–3)
Barren and very sparsely vegetated land	–	–	2.11 (2–10)

keep its basic niches. It was noticed that by 2070, the maximum temperature of the warmest month would be the most important energy-related variable for the expansion of its fundamental niche, while the maximum rainfall of the wettest month and the seasonality of rainfall would be essential for the maintenance of its core niche areas. Non-bioclimatic factors identified as contributing to its niche expansion include excess salt, range (diversity), urban land, and land used for housing and infrastructure (Table 7).

Table 8 IUCN categories: extent of occurrence and area of occurrence of *T. undulata* quantified with different climatic and non-climatic predictors using values of optimum habitat suitability class
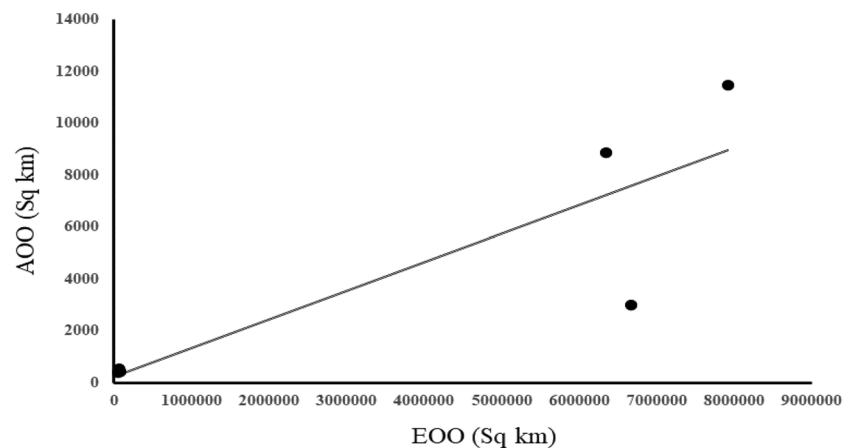
Variables	Current	2050 RCP 4.5	2070 RCP 4.5	Soil	HHI	LULC
EOO (Sq. km)	78,927	58,956	71,594	7,917,441	6,665,913	6,346,060
AOO (Sq. km)	436	376	516	11,476	3008	8856
Number of unique occurrences	109	94	129	4369	752	2214
Number of sub-populations	109	94	129	245	752	493
IUCN annotation (category code)	LC or NT B1a + B2a					
Category EOO and AOO	LC or NT					

EOO extent of occurrence, *AOO* area of occupancy

Automated conservation assessments (AA): I and II

The outcomes of the IUCN's EOO and AOO conservation strategies, as well as other parameters, are displayed in Table 8. EOO of *T. undulata* species, based on climatic and non-climatic predictors, indicates that it should be of the least concern due to the optimal location of its habitat. Soil predictors recorded the largest EOO (7,917,441 km^2), while the 2050 climate time-frame recorded the smallest (58,956 km^2). With regards to the interpretation criterion pertaining to AOO, it is plausible to categorize this particular species as endangered with current and 2050 climatic time frame as their respective AOO values 436 and 376 sq. km. While with 2070 climatic projections, AOO values were lesser than 1000 km^2 but greater than 500 km^2, putting this species in the vulnerable category. Further non-climatic variables also revealed higher numbers of unique occurrences and number of subpopulations as compared to climatic variables and both these variables were recorded minimum with 2050 (Table 8). Significant linear relationship was recorded between EOO and AOO which can be equated as $AOO(Sq.Km.) = 0.001 \times EOO(Sq.Km.) + 232.42; R^2 = 0.74^*$ (at 95% Probability level; Fig. 12).

Percent indigeneity

Based on the number of polygons (the number of sites occupied by this species) and the total occupied area under the specific suitability class, the percentage of indigenous (PI) were calculated for this species, and the results are displayed in Fig. 13. First proposed here, this index works on the premise that a higher value indicates a greater likelihood of this species' generalizability, while a lower value indicates that this species is confined to a smaller area. All four habitat types (optimum = 0.21, moderate = 0.63, marginal = 0.40, and low = 0.21) show a similar pattern with LULC, suggesting a more generalized distribution. Other variables within the optimal class have shown lower PI values, indicating a contraction to a smaller region.

Discussion

The burgeoning interest in Ecological Niche Modelling (ENM) can be attributed to its extensive utilization in gauging the comparative viability of habitats, known and unknown, that have the potential to foster the growth of the species under consideration (Nagaraju et al. 2013; Sen et al. 2016). In addition to its fundamental utility, ENM

Fig. 12 Relationship between EOO and AOO with all the predictors

Fig. 13 Percent indigeneity of *T. undulate* under four habitat suitability classes
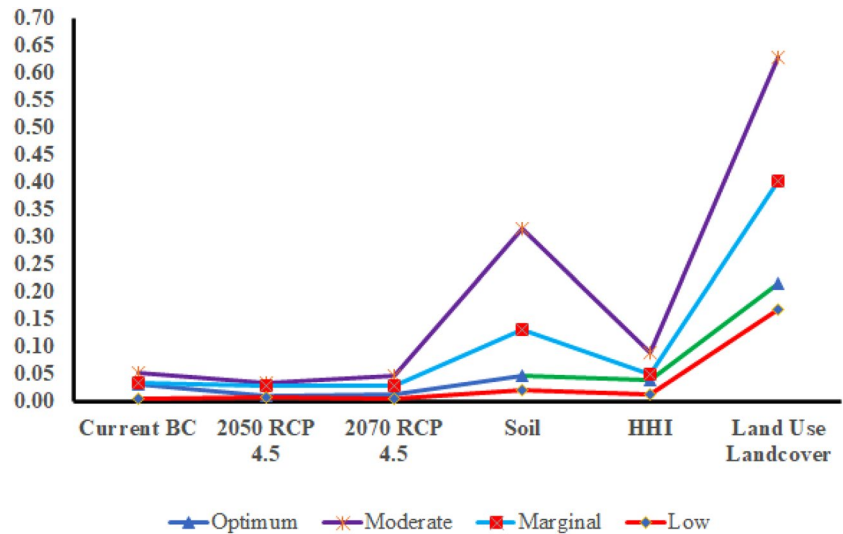
tools are progressively being employed in diverse domains, such as monitoring the propagation of non-indigenous species (Sharma et al. 2018; Ahmad et al. 2019), investigating the adaptive potential of species in response to climate change (Kumar et al. 2020; Mathur et al. 2023), and ascertaining the indigenous distribution of a given species (Joshi et al. 2017).

The utilization of the MaxEnt model by Indian researchers has yielded fruitful results in predicting the potential distribution of endangered plant species in forthcoming times (Boral and Moktan 2021; Chandra et al. 2021; Dhyani et al. 2021; Hussain Mir et al. 2020; Shankhwar et al. 2019; Pownitha et al. 2022; Rawat et al. 2022). Research endeavours in this domain have predominantly taken place in areas characterized by copious rainfall and a rich variety of flora and fauna, such as the Western and Eastern Ghats, as well as the Himalayan region of India. It is arguable that a more pragmatic approach would entail the development of models that accurately capture the ecological niches of endangered plant species that are indigenous to hot arid and semi-arid regions, where resources are characterized by intermittent pulses rather than a steady stream of sustenance (Mathur and Sundarmoorthy 2019). The present study utilized a particular methodology to explicate the distributional patterns of *T. undulata*, along with the factors that impose a spatial and temporal impact on the aforementioned patterns.

Notwithstanding its prevalent application in customary agroforestry methodologies, *T. undulata* faces the peril of extinction in the dry regions of Pakistan and India (Plummer 2021). The dwindling population of the species in their natural habitats can be attributed to various factors such as unlawful deforestation, excessive utilization, and fragmentation of their habitat. Additionally, the species' eco-physiological, reproductive, and dispersal characteristics have

also contributed to this decline (Tripathi and Jaimini 2002; Arshad et al. 2022).

Maxent modelling by Arshad et al. (2022) found that wettest quarter's mean temperature, the warmest quarter's precipitation, and the driest quarter's mean temperature all had significant impacts on the distribution of this species in Pakistan's desert region. According to their findings, highly favorable regions for *T. undulata* were likely to expand, while less favourable areas were predicted to shrink, under any reasonable projection of future climate. Their finding was based on two climatic projections (2050 and 2070 with 4.5 and 8.5 RCPs) with 66 occurrence sites.

A total of 155 presence locations, spread across India, were used for this study to account for the possible existence of the species in question. In contrast to the research conducted by Arshad et al. (2022), the present study employed a distinct set of predictors, incorporating both climatic and non-climatic variables (present, 2050, and 2070, soil and community as well as LULC variables). Several additional variables were subjected to analysis prior to formulating inferences regarding our ecological niche modeling outcome. These included kernel density, niche hypervolume, niche overlap, and IUCN conservation criteria, namely extent of occurrence (EOO) and area of occurrence (AOO), alongside percent indigeneity. The results of these analysis provided conservationists with vital insights into the species' distribution and the measures that should be taken to ensure its continued existence.

With the exception of HHI, our model's qualities were excellent with all predictors. This study also demonstrated that both energy and water variables, specifically annual precipitation, maximum temperature of warmest month, mean temperature of warmest quarter, and precipitation of wettest month, influenced the distribution of this species. According to this ENM analysis, the wettest month's precipitation will

only have an impact with 2070 RCP 4.5. While the remaining three variables are operational for *T. undulata* with subtle changes in their range, for example, annual precipitation, which is the primary factor with current conditions, supports its peak suitability with a range of 300 to 500 mm, this variable during 2050 RCP 4.5 effectively controls its suitability with a range of 400 to 600 mm. Such trends, which were also recorded for the maximum temperature of the warmest month, which is a prime factor under current and 2070 conditions, support its optimum suitability with 40–43 °C and 45–50 °C, respectively. Such quantitative information is crucial because our research shows that climatic conditions, as opposed to other non-climatic variables studied, severely restrict the range of this species to a specific semi-arid climate zone in India. Therefore, it is of utmost importance for restoration and plantation programs to comprehend the critical limits of such critical factors.

Conditions for rooting include an adequate depth of soil and an adequate amount of soil after accounting for the presence of burial ground stones. It has a number of effects on plant development, such as root development, nutrient availability, and root anchorage. In contrast, the soil's texture, minerals, organic carbon, pH, and total exchangeable bases were all included in the used data set for determining nutrient availability (FAO 2012). According to Fischer et al. (2008) qualitative criteria for assessing soil quality, where 2 denotes moderate restrictions, 3 indicates severe limitations, and 4 indicates very severe limitations. This species' habitat appropriateness was found to be moderately to severely impacted by rooting conditions, nutrient availability and excess salts in this study as demonstrated with response curves. The conspicuous nonexistence of this particular species in soil that is abundant in nutrients substantiates these conclusions, implying that it is a viable contender for reforestation and restoration in environments that are deficient in nutrients. The findings of Kumar et al. (2011), Kumar and Kumar (2014), and Bania and Sheoran (2021), who employ this species in the rehabilitation of lignite mine backfill in Giral mines Barmer, Rajasthan, India, corroborate these conclusions. According to research conducted by Zolfaghari et al. (2017), the distribution of *T. undulata* is most strongly influenced by neutral pH, 5.35 ds/m soil electrical conductivity, soil phosphorus, and bulk density in sandy and loam sandy soils. Soil phosphorus has been studied for its facilitation behavior on the height, girth, and crown spread of this species by Gupta et al. (1996) and Dutta et al. (1997). The results of our study also underscore the importance of the presence of essential minerals and nutrients, as well as salt levels, in the root zone. The findings of this research possess versatile implications, including but not limited to the administration of rare arboreal species preservation, the ranking of regions for the purpose of propagation and cultivation, and the detection of unexplored sites that could potentially harbor *T. undulata*.

Numerous scholarly investigations have demonstrated a direct correlation between the diversity of life forms and the ecosystem's capacity to provide essential services, which is inextricably linked to the prevalence of heterogeneous habitats within the landscape. The intricate dynamics of meta-populations and meta-communities arise from the interplay between the diverse array of habitats present in a given landscape and the competitive pressures that ensue among them. In accordance with the tenets of niche theory, a locale characterized by greater heterogeneity may afford a greater degree of niche space, thereby facilitating the coexistence of a greater number of species through niche partitioning. Consequently, it stands to reason that an area exhibiting greater diversity should exhibit a commensurately higher diversity of species. Our model shows that range, maximum, and coefficient of variation are most important for *T. undulata*, and the ROC curves for these three parameters indicate that there is a high peak of habitat suitability of this species at a somewhat wide base that narrows to a set of values. Our findings are consistent with the synthesis of Loke and Chisholm (2022), who described the characteristics of complex systems as including a wide variety of interacting elements, a hierarchical organization, the formation of new patterns, and other traits.

Xerophytes such as *Prosopis cineraria* (L.) Druce, *Zizyphus* spp., *Salvadora* spp., and *Capparis decidua* (Forssk.) Edgew. coexist with *T. undulata* in dry and semiarid regions of India (Singh 2009; Mathur and Sundarmoorthy 2013). This tree species has been widely recommended for restoration projects in sandy areas and along canals to lessen sand build-up in these places because of its effectiveness at stabilizing sand dunes and its ability to function as a shelter belt (Upadhyaya 1991; CAZRI 2021). This research also shows that it can thrive in a wide variety of ecosystems across India, and that among the HHI predictors, range variables would aid in the establishment of a stable niche for it to grow in. The hump-back relationship between the probability of occurrence of this species and evenness among the community variables suggests that it can be accommodated with other associates without altering community structure and function due to its lack of allelopathic traits and the facilitation of sharing resources with other community resources (Singh et al. 2004; Tewari and Singh 2006). Coefficients of variation used to assess diversity agree with these findings, making the Enhance Vegetation Index a top pick for reforestation, rehabilitation, and restoration projects that aim to increase the variety of plant life in a given area (Kumar et al. 2011).

Land use/land cover changes (LULCCs) are the end outcome of a complicated interplay between demographic shifts, technological advances, biophysical limitations, and

past land usage. A system's resilience can become unbalanced as a result of their actions, which span a wide range of time and space and involve shifts toward distinct ecological roles as well as fluctuations in intensity within a function (Bajocco et al. 2015). While land cover provides accurate small-scale information on habitat fragmentation and human influence that is not represented in other more regularly used bioclimatic variables, it is also considered relevant in ecological niche modelling seeking to predict species distributions (Tasser et al. 2017). The current study found that LULC had a more significant impact on habitat suitability than bio-climatic variables, which runs counter to the findings of Chauvier et al. (2021) and Rathore et al. (2022), who found that climatic variables had a much larger effect on the spatial distribution of plant species than soil and LULC factors. Yet, both of those reports come from higher altitude regions. Current research allows us to conclude that LULC is more successful at the species level than bio-climatic factors, in particular as they relate to urban land, land used for habitation and infrastructure, and forest, as well as barren or extremely sparsely vegetated land. These factors are directly related to the ecological requirements of this species, which is commonly found in the forested areas of Rajasthan and Gujarat, as well as in the open grazing areas, which typically have a smaller community associated with them. Human activities such as cutting, grazing, and infrastructure development are limited in each of these regions, hence support its population indirectly.

Tecomella undulata distribution is significantly constrained by climatic variables, whereas soil, community and LULC variables suggest a more conducive nature for this species, as evidenced by the greater spatial extent of each habitat class with these two variables. Such findings are corroborated by our niche overlap, which was smaller (both D and I) with non-climatic predictors. Low niche overlap, which implies unequal resource consumption, is thought to be necessary for the coexistence of syntopic species and thus the promotion of permanent diversity.

Our research indicates that the optimal region for the survival of this species' natural populations will drop by 3550 Sq. Km. by the year 2050 and increase by 8331.0 Sq. Km. by the year 2070 due to climate change. These results are comparable with those found by Pownitha et al. (2022) for the critically endangered *Coscinium fenestratum* and the *Embelia ribes*, both of which live in the Western Ghats of India.

Eco-physiological research on this species would allow us to glean the cause-and-effect relationships that have led to its geographical contraction and forced survival in the western parts of the country due to climatic factors. Zolfaghari and Mordi (2018) reported an aggregated or clumped pattern of *T. undulata* stands in the Bushehr region of Iran, which may be related to dry conditions and a lack of moisture, and showed that it was more resilient in the wild. A profound comprehension of the biology and phenology of seeds is a prerequisite for the perpetuation of this particular organism. Through the acquisition of knowledge pertaining to these dual aspects, ENM models can be enhanced. The findings of the current study suggest that conservation efforts ought to consider the species-specific traits in relation to their spatial and temporal distribution, which is influenced by various factors such as climate, soil, community, and land use and land cover (LULC) predictors. Given the current lack of viable techniques for the vegetative propagation of this particular species (Bhansali 1993; Amiri et al. 2019), it is imperative that high-grade seeds be utilized for extensive plantation efforts (Jindal and Bhansali 1997). Seeds can be found between April and June. However, it is possible to find unripe or overripe capsules (Jindal et al. 1987). Fruits that were mature in April had a higher chance of germinating than those that were mature in June (Jindal et al. 1990). At 35 °C, newly collected seeds sprouted 82% but 2-year-old seeds germinated just 15.50%. Besides germination rate, storage affects seedling vitality. It's flower season from about November to March. The peak bloom time was between the end of February and the middle of March. There were multiple times when fresh flowers appeared on the same tree (Arya and Shekhawat 1986; Arya et al. 1992; Tripathi and Jaimini 2002). Fruit set percentages varied from 0.64% when self-pollinated to 3.94% when cross pollinated, indicating self-incompatibility despite the absence of apomixis. Due to its morphological adaptations for cross pollination, such as its large, showy flowers, abundance of pollen, floral polymorphism (color), and extended flowering period, *T. undulata* is a cross-pollinated plant (Jindal et al. 1985). Between the hours of 6 a.m. and 12 p.m., bisexual flowers undergo anthesis. An hour after anthesis, dehiscence begins (Tripathi and Jaimini 2002). The foregoing knowledge can aid ecological niche modelling-based conservation initiatives. This research also has two potential future assessments: (a) performing ground-truthing in the unreported areas to validate results; and (b) conducting the research with an ensemble technique that can balance the merits and drawbacks of using different algorithms, such as random forest, artificial neural network, and support vector machine (Mathur and Mathur 2023).

Conclusions

Due to its usefulness in determining the potential suitability of known and unknown locations for the cultivation of the species in question, interest in ENM has increased in recent years. Our Maxent model for predicting the distribution of *Tecomella undulata* was highly accurate, taking into account both bio-climatic and non-bioclimatic factors. The study highlights the significance of mean and maximum

temperatures during the warmest quarter and month, as well as the precipitation of wettest month. Compared to climatic variables, which restricted this species' range to a narrow band of arid and semi-arid environment, soil, habitat heterogeneity indices (diversity), and LULC predictors showed more facilitation behavior of *T. undulata*, allowing it to spread in larger areas across the India. Diversity parameters showed high levels of spatial randomness (NoPs) for moderate, marginal, and low habitat types, soil variables were found to be in control of such a pattern in the optimum area. The consequent change in habitat quality from low to moderate area can be understood as a result. Rooting conditions, nutrient availability, and salt concertation are all important factors in determining *T. undulata's* optimal suitability after it has overcome any barriers posed by the composition of the community. However, research into population dynamics has shown that this species can thrive in low-nutrient environments. This study indicated that soil variables make the entire state of Rajasthan a favorable habitat for *T. undulata*. HHI provides nearly uniformly good environments for this species. It can be deduced from the findings of this study that the current annual precipitation is conducive to the expansion of its ecological niche, while precipitation of the wettest quarter and maximum temperature of the warmest month will support its niche expansion in the 2050 and 2070 periods, respectively. Based on projections, it seems that Indian states like Rajasthan and Gujarat are home to this species. This research also pinpointed the Churu and Jhunjhunu districts and a transact region encompassing Pali, Jalor, Jodhpur, Sanchor, and Barmer as promising areas within Rajasthan for the survival of this species. Population shrinkage would begin around 2050 in all of these areas. Churu, Jhunjhunu, and Jodhpur were the hardest hit by this decrease. By 2070, the Churu and Jhunjhunu regions had become significantly more fragmented, while the Jodhpur region and the surrounding areas of Barmer, Sanchor, Jalor, and Vav had grown. Previous efforts to rehabilitate lignite mine backfill in arid areas at Barmer with this species and their subsequent survival and success are bolstered by the findings of the current study, which shed light on nutrient availability, rooting conditions, and excess salt. Climate characteristics, seed biology, and phenological event ecophysiology were all discussed. The findings would have helped improve *T. undulata* conservation and management efforts. The results of this research can be used to create strategies for the commercially important tree planting, replanting, and management of agroforestry in the region.

Author contributions Senior author conceptualized the chapter theme and interpretation of output of various machine learning techniques. Co-Author prepared various types of language codes in python, Java and in R scripts and convert the various file format from ASCII to KML, Raster, dbf, CSV etc. for software's like QGIS 3.10.0; Wallace;

DIVA-GIS version 7.5; MaxEnt 3.4.1 software; SDM toolbox; Map Comparison Kit; ENMTools and Ntbox; SSDM R packages.

Availability of data and materials The data sets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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