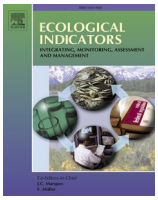
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Species distribution models to predict the potential niche shift and priority conservation areas for mangroves (*Rhizophora apiculata, R. mucronata*) in response to climate and sea level fluctuations along coastal India

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ABSTRACT

Mangroves are more than just a tree as they are home to thousands of species, carbon absorbers and a natural coastal fortress against floods and storm surges. Hence, conservation planning and decision making for this valuable ecosystem must involve identification of priority conservation areas (PCAs) at species-specific dimensions. In the present study, we adopted an ensemble modelling approach for the distribution of two mangrove species (*Rhizophora apiculata*, *Rhizophora mucronata*) using high-resolution environmental and edaphic datasets, to identify the PCAs for future conservation. We also identified the key environmental variables shaping their distribution and precisely estimated the core distributional shift along the Indian coastline under changing climate scenario. The findings revealed that about 5844 km^2 and 7846 km^2 areas were identified as extremely suitable areas, which were distributed along Maharashtra coast and Kerala coast for *R. mucronata* and *R. apiculata*, respectively, in the current climate scenario. The distribution of *R. apiculata* was found to be mostly shaped by mean diurnal range and annual mean temperature, whereas the distribution of *R. mucronata* was primarily shaped by annual mean temperature and altitude. The highest range expansion of mangrove species occurred during middle Holocene due to high precipitation and sea-level rise and this finding is further supported by fossil pollen evidence. The suitable habitat range for *R. apiculata* is predicted to increase along Kerala coast under RCP2.6 scenario by 6.90% and 6.93% and under RCP8.5 scenario by 9.33% and 9.90% in the year 2050 and 2070, respectively, whereas the range for *R. mucronata* is getting reduced in the future climate scenario. Overall, our predictions reveal a steady migration of conducive mangrove habitat towards land or higher elevations due to relative sea level rise in future. These results would aid in planning a long-term species-specific conservation and management strategy for mangrove ecosystem along coastal India.

1. Introduction

Mangroves are a unique ecosystem comprising of the intertidal marine plant community that predominates the margins of tropical coastlines all over the world. They offer a variety of essential services to human communities and the biosphere, including the flood control, filtration of water, preservation of wildlife habitat, reducing the effects of climate change and preserving cultural values (Cao and Fox, 2009; Zhang et al., 2021). They also make up 20– 30% of the global carbon pool, making them essential for carbon sequestration and controlling impacts of changing climatic condition (Kayranli et al., 2010). They typically store thrice as much carbon as comparable terrestrial forests do. Yet, mangroves are today severely threatened by anthropogenic activity and climate change, resulting in a sharp decline in their range and extensive degradation (Zhang et al., 2021; Samal et al., 2022). It is projected that coastal vegetation will be significantly impacted by climate change through direct biophysical regime impacts such as drought, changing rainfall patterns and overheating, and also indirect effects such as wildfires, changes in land cover and sea level rise (Dwire et al., 2018; Middleton, 2012). Meanwhile, because of the agricultural activities, >50% coastal wetlands are getting reduced worldwide (Verhoeven and Setter, 2009). Especially in Asia, about 30–50% of coastal

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wetlands have degraded over the last three decades (Alongi, 2015).

One of the most significant mangrove genera in the tropical region is *Rhizophora*, commonly occurring in the tidal creeks. In terms of benefits of this genera, it serves as coastal guard by protecting the coastal ecosystems from tsunamis, storms and hurricanes (Alongi, 2008). It also prevents coastal erosion due to its roots' ability to capture suspended solids, wherein the upland runoff is filtered, preserving sea grass beds and coral reefs from the damaging effects of the suspended solids (Alongi et al., 2005; Alongi, 2008). Additionally, because of its extensive prop root systems, aquatic organisms such as fish and prawns can reproduce and the juveniles can find shelter (Negelkerken et al., 2000). Apart from its ecological and economic benefits, it also has medicinal attributes for its traditional usage to treat ulcers, hepatitis, haematoma, and elephantiasis (Ravikumar et al., 2005).

These stilt mangroves occur widely throughout the Indo-west pacific region along the tropical and subtropical intertidal wetlands. The target species i.e. *R. apiculata* and *R. mucronata* are widely distributed along the West Bengal, Odisha, Andhra Pradesh, Tamil Nadu, Kerala, Karnataka and Gujarat coast. Precisely, these species are distributed in Bali Island of Sundarban Delta along West Bengal coast, Bhitarkanika, Kansaridia, Khola and Kharnasi region of Odisha coast, Ramannapalem, Chinnavalasala and Gadimoga area of Coringa mangrove region of Andhra Pradesh coast and Pichavaram, Muthupet and Gulf of Mannar along Tamil Nadu coast on the east coast of India. Similarly, the current occurrence of these species is widely distributed in Kannur and Ernakulam districts of Kerala coast, Tarkarli, Achara and Kolamb area of Konkan region and also along Gorai creek of Mumbai of Maharashtra coast along the west coast of India. However, along the Gujarat coast only *R. mucronata* is found along Gulf of Kachchh, Gulf of Khambhat, Kori creek and Purna estuary region. Although they appear to have continuous distributions, different species within the same genus have distinct preferred zonation throughout coastal habitats, where they are dominant. *Rhizophora mucronata* grows in regions experiencing regular freshwater flows, *Rhizophora stylosa* is mainly found in marine conditions and prefers exposed offshore areas, *R. apiculata* is encountered in embayments and mid-lower sites of large riverine estuaries while the hybrid species *R.* × *lamarckii* has been located from mid-high intertidal regions of estuaries (Duke, 2006). These stilt mangroves flourish in subtropical and tropical climates with somewhat high and evenly distributed rainfall. Their distributional range, form and biomass are a reflection of their response to variations in the temperature and precipitation pattern through time and space. As these mangroves are limited to elevations between the highest tides and mean sea level, their communities will need to relocate inland during the time of sea level rise. As a result of the responses of these mangrove habitats and their distributional shift, these crucial climate change markers may be recognized and mapped. Accurate understanding of these shifts and their root causes enables more accurate forecasting of upcoming changes.

The IPCC's Fifth Assessment Report (AR5) predicts that global warming will continue, with an average increase in temperature of 0.3 to 4.5 °C by 2100 compared to 1986 to 2005. Later, the Intergovernmental Panel on Climate Change (IPCC)'s Working Group One (WG1) issued the Sixth Assessment Report (AR6), which states that the rise in global surface temperature during the period of 1850–1900 was 1.09 °C (0.95°–1.20 °C) for the decade 2011–2022 (Arias et al., 2021). The report also states that, the rise is expected to increase by 1.0 °C- 1.8 °C in the lowest CO_2 emission scenario and 3.3 °C- 5.7 °C in the highest CO_2 emission scenario for the period of 2081–2100 in comparison to 1850–1900. Climate change remarkably affect the species diversity and their distributional changes will consequently show how change in climatic condition has impacted the landscape (Lawler et al., 2009; Zhang et al., 2021). Hence, species-specific knowledge of responses of mangrove to climate variability and sea level changes would aid in formulating more accurate management and conservation strategies in the high priority suitable habitats.

Species distribution models (SDMs) are the key tool to understand the association between species and its environment and also predicting species response to such environmental changes (Elith and Leathwick, 2009; Elith and Franklin, 2013; Sahana et al., 2022). The power of SDM to forecast the potential geographical distribution of the species in future time periods facilitate numerous ecological applications, such as predicting the highly suitable habitat under different climate change scenarios (Pearson and Dawson, 2003; Hijmans and Graham, 2006; Kaky et al., 2020), helping with conservation and management plans, and also providing information about the ecological preferences, paleobiology (Svenning et al., 2011) and biogeography (Guisan et al., 2006). For the sake of forecasting distributions of the species based on environmental factors, an extensive variety of SDM techniques have been designed (Thuiller, 2003). Frequently utilised algorithms are; maximum entropy modelling (MaxEnt) (Phillips et al., 2006), generalized additive models (GAM) and generalized linear models (Guisan et al., 2002; Hastie and Tibshirani, 2004), boosted regression trees (brt) (De'Ath, 2007), random forests (rf) (Svetnik et al., 2003) and other machine learning algorithms such as Bayesian hierarchical modelling (Latimer et al., 2006) or artificial neural networks (ANN) (Zurada, 1992). Many of these techniques are simple to apply concomitantly in statistical programmes and packages, and generally, the frequently used algorithms have the more user-friendly and simple interfaces (Norberg et al., 2019). The sample size, spatial distribution, choice of predictor variables, and the SDM method, are possible causes of uncertainty in predictions, each of which can affect predictive power and accuracy of the model (Buisson et al., 2010). To overcome these uncertainties, based on evaluation metric e.g. AUC, ensemble model has been used in the present study that integrate prediction of single SDM model outcomes into one average binary map (Thuiller et al., 2004).

Despite its socio-economic value, mangrove ecosystems are at a risk of extinction, particularly in developing countries (Friess et al., 2020). Loss of suitable habitat of mangroves in countries like Malaysia and Myanmar exceeds the global average, where proper conservation measures should be planned (Friess et al., 2020). Several studies have been conducted to map the potential distribution of mangroves in future climatic scenarios globally as well as regionally (Dang et al., 2021; Banerjee et al., 2021; Sahana et al., 2022; Samal et al., 2022). Banerjee et al. (2021) have suggested prioritizing sites for both true mangroves and mangrove associates in the Indo-West Pacific region. However, the species-specific response to the future climate change in a developing country like India is still missing. Hence in the present study, we tried to assess the niche distribution and environmental factors responsible for shaping the distribution, for which we adopted ensemble modelling approach to predict the habitat suitability of two *Rhizophora* species (*R. apiculata* and *R. mucronata*) in Indian subcontinent using a widespread collection of occurrence records. The key objectives of the present study are: (1) to identify the significant bioclimatic and edaphic factors influencing the niche range shift of *Rhizophora* species; (2) to evaluate the core distributional shift of these species in past (Mid-Holocene), present and future (2050, 2070 under RCP 2.6 and RCP 8.5 i.e. the two greenhouse gas emission scenarios and (3) to measure the spatial extent of the habitat suitability for both *Rhizophora* species in future climatic condition so that it will help to plan a more precise species specific conservation strategy in different sectors of the Indian coastline.

2. Materials and methods

The methods employed in this study include:

1. Compiling species occurrence record and the environmental datasets.
2. Predicting the habitat suitability of two *Rhizophora* species i.e. *R. apiculata* and *R. mucronata* based on ensemble modelling by using *sdm* package available in R software.

3. Identifying the pattern of the centroid shift of the suitable habitat area using SDM toolbox version 2.5.

A detailed workflow of the analyses used in the present study has been outlined in (Fig. 1).

2.1. Species occurrence record

Species occurrence points are the geographic points (latitude and longitude) where a species has occurred. In an ensemble model, these records provide crucial information for predicting habitat suitability. The geo-referenced occurrence points for *R. mucronata* and *R. apiculata* have been compiled after a thorough literature survey conducted using databases i.e. Global Biodiversity Information Facility (GBIF, 2023) database (10.15468/dl.aq8r9con January 16, 2023) and published literatures. Globally 6298 and 2478 occurrence points have been compiled from GBIF for *R. apiculata* and *R. mucronata* and processed for the Indian subcontinent using ArcGIS 10.5. The occurrence records were spatially rarefied and filtered within a grid cell of 10 km × 10 km by using SDM toolbox version 2.5 available in ArcGIS 10.5. At the end of the process, a total 67 (Fig. 2) and 101 (Fig. 3) presence records were used in constructing the models.

2.2. Environmental variable selection

Based on the environmental factors that can potentially affect the distribution of *R. apiculata* and *R. mucronata*, total 27 environmental variables were selected to model the current distribution pattern of these species. Amongst these, a total of 19 bioclimatic variables were compiled from Worldclim database, version 1.4 (https://www.worldclim.org/) (Hijmans et al., 2005) with 30 arc-seconds spatial resolution (*c.* 1 km^2 area). Seven soil parameters such as soil pH, soil organic carbon stock (SOCS), bulk density (BD) of fine earth fraction, organic carbon density (OCD), proportion of clay content (CC), cation exchange capacity (CEC) and total nitrogen (TN) were extracted from the SoilGrids™ database version 2.0 (de Sousa et al., 2020). Lastly, one topographical variable i.e. elevation has been added to project the niche range of these species.

From the general circulation model (GCM), coupled model intercomparison project (CMIP5) were downscaled and verified using the baseline climate from Worldclim 1.4, which has been often used in earlier research, for the projection of past, current and future climate (Hu et al., 2020; Banerjee et al., 2022; Samal et al., 2022). Further, from the GCMs, Hadley Global Environment Model 2-Earth System (HadGEM2-ES) was used to model the future climate scenarios. Two representative concentration paths (RCPs), i.e., RCP2.6 (lowest) and RCP8.5 (highest) greenhouse gas concentrations reported by IPCC Assessment Report 5 (AR5), were used for past (~ 6000 years ago), and future (for the year 2050 and 2070) prediction. Following the assessments of SDM projection under past and future climatic condition, the 7 soil parameters (pH, OCD, SOCS, BD, CC, CEC and TN) remained unchanged. The overall spatial resolution of these environmental factors was compiled to 30 arc-seconds spatial resolution (*c.* 1 km^2 area).

It is advised to eliminate the highly correlated variables before adding the environmental variables to model the species distribution (Graham, 2003). We executed collinearity test of these environmental variables through *usdm* package in R software (Naimi et al., 2014), to remove the highly correlated variables. Variables having the variance inflammation factor VIF > 10 along with the Pearson correlation coefficient ≥ 0.7 were removed (Dormann et al., 2013). A list of the resulting variables were provided in Table 1.

2.3. Development and validation of model

An ensemble modelling approach were adopted in this study to predict the ecological niche for *R. apiculata* and *R. mucronata*. We used eight modelling algorithms from the *sdm* package available in R software (Naimi and Arajo, 2016). A number of statistical methods with various characteristics and levels of complexity offer a range of potential projections, and it has frequently been shown that an ensemble of methods chosen in accordance with the evaluation criteria gradually enhances the transferability of models (Guisan et al., 2017). These model includes: two classification algorithms, classification and regression trees (RPART) (Therneau and Atkinson, 1997), and flexible discriminant analysis (FDA) (Hastie et al., 1994); a maximum entropy algorithm-MAXENT (Phillips et al., 2006); a climatic envelope approach

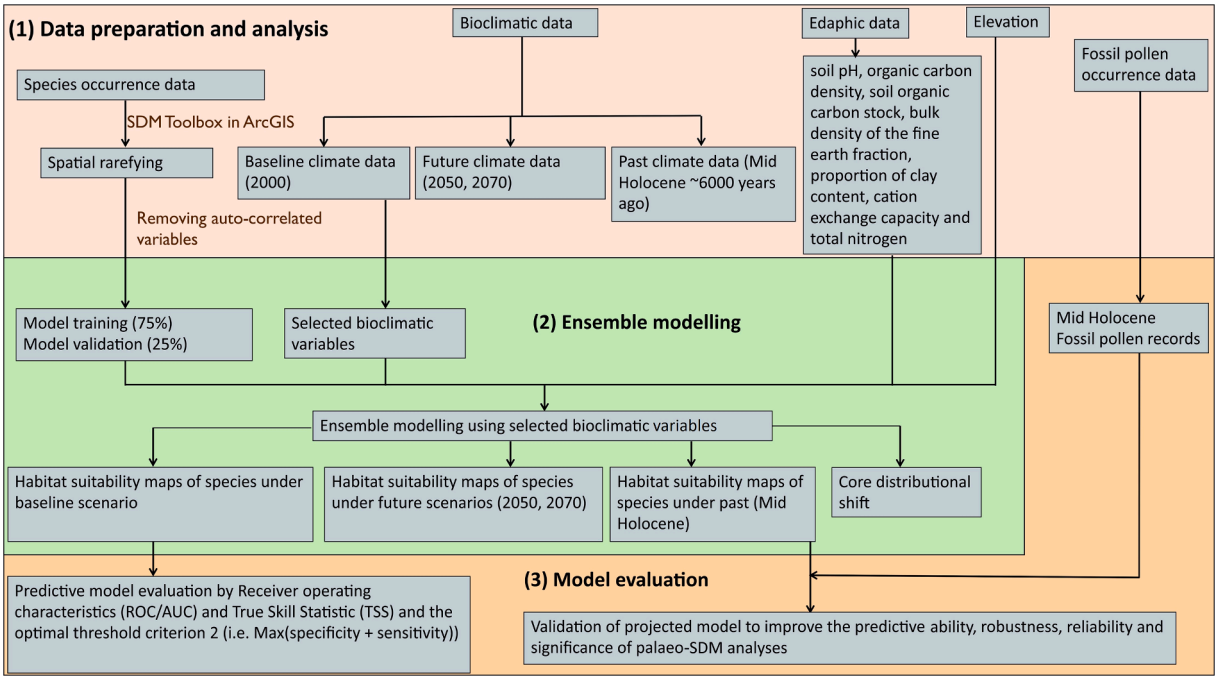


Fig. 1. Methodology in flow diagram.

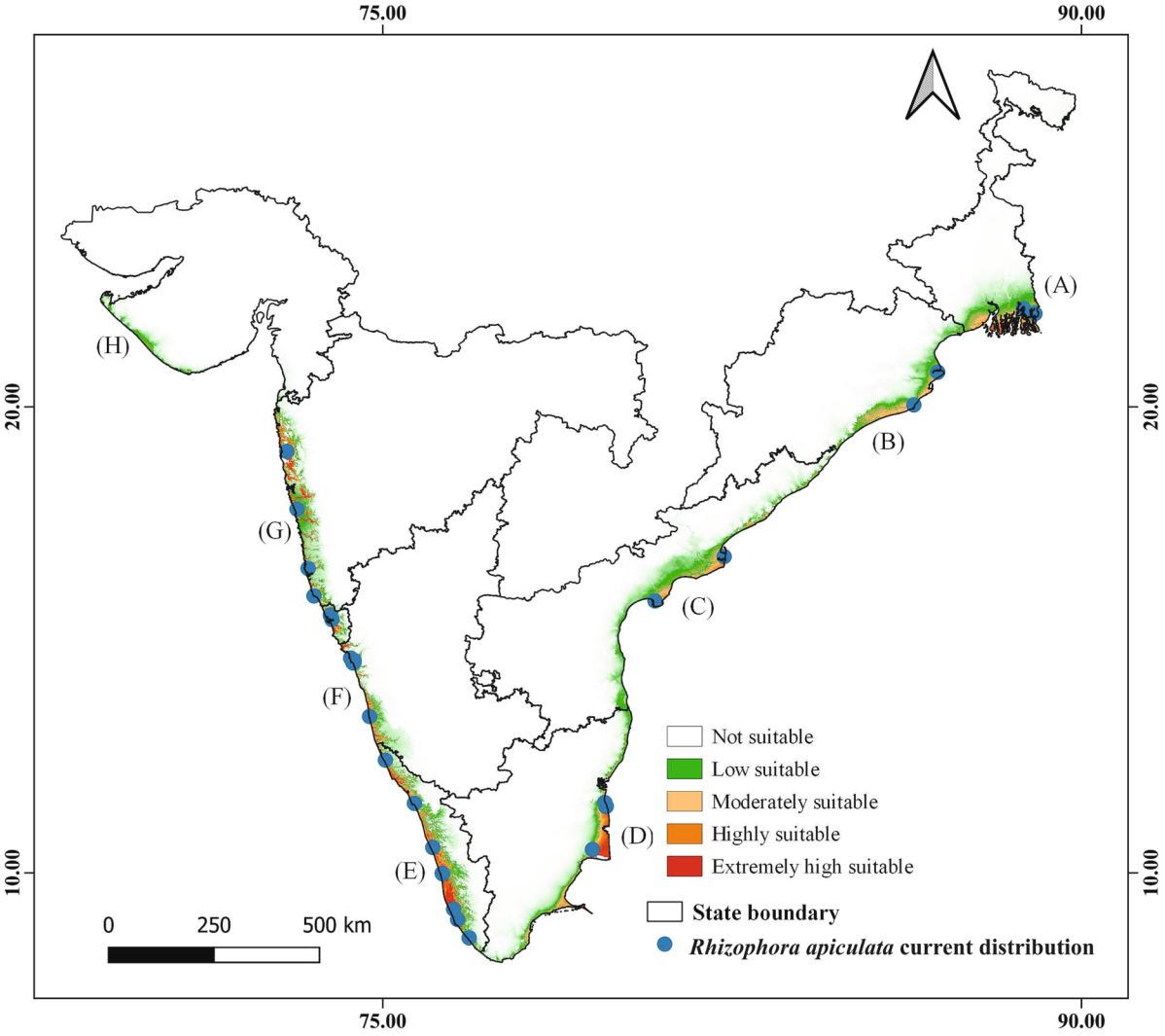


Fig. 2. Current occurrence records of *Rhizophora apiculata* along (A) West Bengal (B) Odisha (C) Andhra Pradesh (D) Tamil Nadu (E) Kerala (F) Karnataka (G) Maharashtra (H) Gujarat coast.

(BIOCLIM) (Busby, 1991); two modern machine learning approach, random forests (RF) algorithm (Breiman, 2001), and support vector machine (SVM) (Vapnik, 1995); and two regression algorithms, generalized linear model (GLM) (McCullagh and Nelder, 1989) and multivariate adaptive regression splines (MARS) (Friedman, 1991).

For each species, the occurrence points were arbitrarily splited into 80% for training and remaining 20% for validating. The background points (30 points) were chosen in R software depending on the environmental variables to enhance the model's accuracy (Senay et al., 2013). The presence data for the species with a background mask was used to generate the background or pseudo-absence data. To strengthen the evaluation of model performance, each algorithm was set to develop 6 models (3 × 2 replication method), thus generating a total of 36 models. To evaluate the importance of each predictor variable and its contribution to the niche shift of these *Rhizophora* species, permutation constructed on two metrics, such as the Pearson Correlation and AUC test, has been used in the *sdm* package.

The model's evaluation robustness was calibrated and validated using threshold-dependent true skill statistics (TSS) (Allouche et al., 2006) and threshold-independent receiver operating characteristics of area under the curve (ROC/AUC) (Fielding and Bell, 1997) available in *sdm* package. Based on the AUC value (ranges between 0 and 1), performance of the model is categorised as excellent (>0.9), good (0.8–09), fair (0.7–0.8), poor (0.6–0.7) and fail (0.5–0.6) (Swets, 1988; Vanagas, 2004). Similarly, based on TSS value (ranges between + 1 and −1), model performance is classified as good to excellent (>0.8), useful (0.6–0.8) and poor (0.2–0.6) (Coetzee et al., 2009; Shabani et al., 2016). In the present study, we constructed an ensemble model using the weighted averaging approach based on TSS statistics and the optimal threshold criterion 2 (i.e. Max (Sens + Spec)). By utilising the 'ensemble' function of the *sdm* package, the models that were successfully fitted were taken into consideration to produce ensemble maps. The final predicted potential distribution for past, current and future (2050 and 2070) of these species had a range value from 0 to 1 which were reclassified into five groups showing extreme suitability (>0.8), high suitability (0.6–0.8), moderate suitability (0.4–0.6), low suitability (0.2–0.4) and no suitability (0–0.2) to climatic and edaphic conditions by using ArcGIS 10.5.

2.4. Core distribution shift

The pattern of change in niche area was also estimated, and the centroid of the shift for past, present and future suitable habitats were compared using a Python-based GIS software i.e. the SDM tool-box (Brown, 2014). This study also demarcates the centre of niche shift of *R. apiculata* and *R. mucronata*. To perform this, the distribution of each species was narrowed down to a centroid (centre) point, and a vector file was produced to show the direction and magnitude of the forecasted

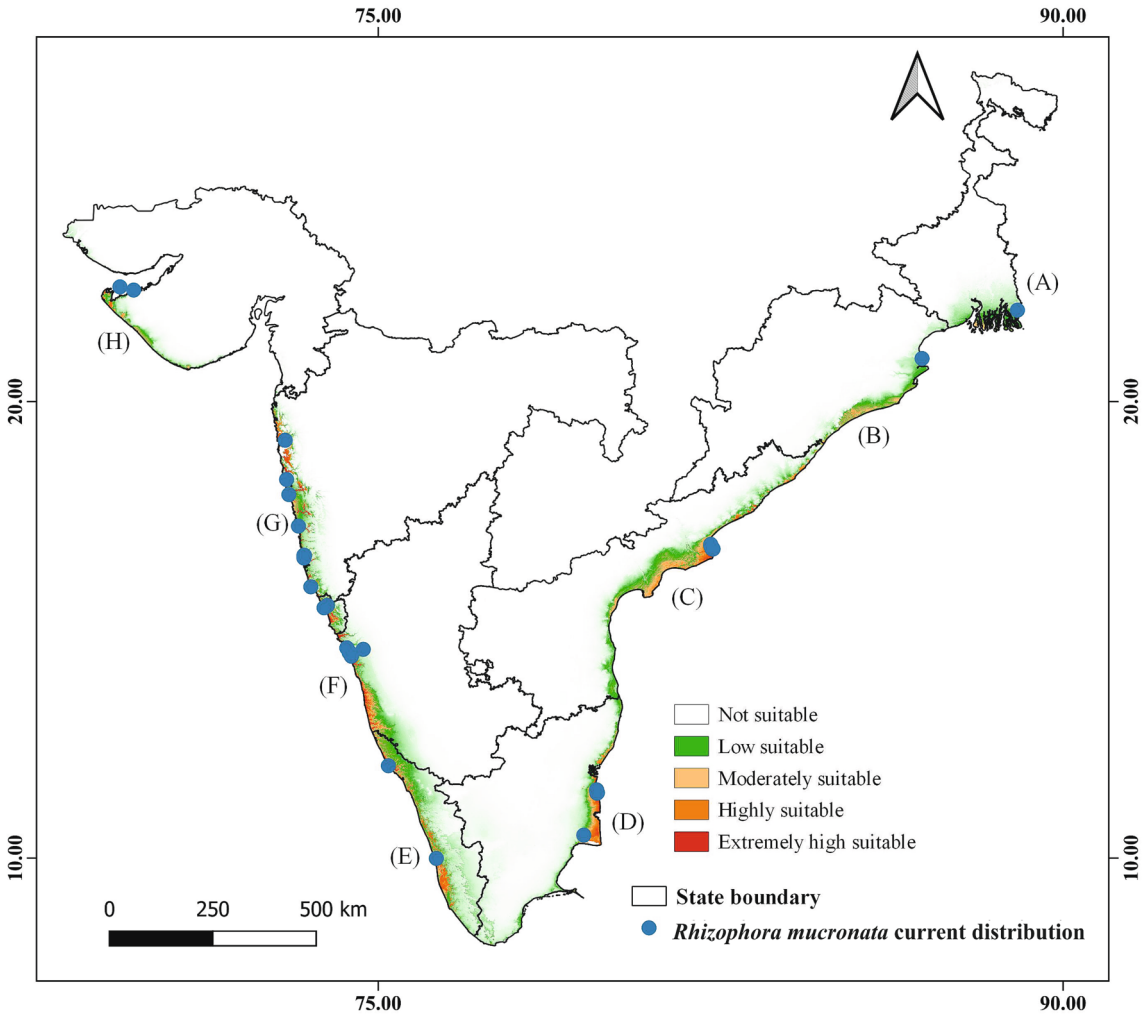


Fig. 3. Current occurrence records of *Rhizophora mucronata*. along (A) West Bengal (B) Odisha (C) Andhra Pradesh (D) Tamil Nadu (E) Kerala (F) Karnataka (G) Maharashtra (H) Gujarat coast.

change over different time slices. Finally, we investigated the changes in the niche distribution by monitoring the shifts in the centre points with various SDMs.

3. Results

3.1. Species distribution and evaluation

The model performance of *R. apiculata* and *R. mucronata* were better than random, with the provided training and testing data set. Based on the AUC and TSS values, the best model performance was produced by *maxent* model for both *R. apiculata* (AUC-1, TSS-1) and *R. mucronata* (AUC-1, TSS-1), however the poor performance was generated by *bioclim* model for both *R. apiculata* (AUC- 0.67, TSS- 0.33) and *R. mucronata* (AUC-0.78, TSS-0.56). The evaluation of ensemble model also depicted that the predicted models for both the species generated excellent model performance with AUC value 0.99 and TSS value 0.967 for *R. apiculata* and with AUC and TSS value 1 for *R. mucronata* (Table 2).

In the current scenario, the evaluated areas of extreme to high suitable habitat for *R. apiculata* included West Bengal, Tamil Nadu (Cauvery Delta), Kerala and Maharashtra (Vasai, Vikroli) coast of the Indian peninsula (Fig. 4a,b). Similarly, the extreme to high suitable habitat for *R. mucronata* occur in Tamil Nadu (Cauvery delta), Andhra Pradesh (Coringa mangrove), Maharashtra (Kundalika, Vikroli) and Gujurat (Dwarka) coast of the Indian peninsula (Fig. 5a,b). The current areas of extremely suitable habitats for *R. apiculata* and *R. mucronata* encompass about 7981 km^2 and 6022 km^2, respectively. Projected past (6000 years BP) distribution depicted that the areas of extreme to high suitable habitat occurred along West Bengal (Sundarban delta), Odisha (Chilika Lagoon), Andhra Pradesh (Coringa mangroves), Tamil Nadu (Pichvaram, Muthupet), Kerala (Vembanad) and Maharashtra (Vikroli) coast for *R. apiculata* (Fig. 6a,b). Similarly, for *R. mucronata* the projected extreme to high suitable habitat included Sundarban delta, Coringa mangrove, Pichvaram and Muthupet (Cauvery delta) and Vembanad of Indian peninsula (Fig. 7a,b). The areas of extremely suitable habitat of past distribution for *R. apiculata* and *R. mucronata* encompass about 21,267 km^2 and 8626 km^2, respectively.

Under RCP2.6–2050 climate change scenario, the ensemble model predicts the increase in *R. apiculata* extremely suitable habitat area in Sundarban delta (3.95%), Mahanadi delta and Chilika Lagoon (1.5%), Coringa mangrove (0.77%), Pichavaram and Muthupet (1.50%), Kerala coast (6.90%) and Udupi region (Karnataka coast, 0.22%) (Fig. 6a,b), accounting to ~ 21,563 km^2. Under RCP2.6–2070 climatic scenario, the increased extremely suitable habitat area remain unchanged in comparison with 2050. Based on the current climate scenario, the overall extremely suitable habitat area are expected to increase by 1.70% and 1.56% under RCP2.6 2050 and 2070 scenario, respectively in the Indian subcontinent. However, in *R. mucronata*, model a loss in extremely suitable habitat area in Coringa mangroves (0.39%), Pichavaram and Muthupet (0.82%), Kerala coast (2.77%), Maharashtra coast (0.33%)

Table 1
Percentage contribution of the environmental variables included to model *Rhizophora apiculata* and *Rhizophora mucronata*. (- indicates removed variables because of their high collinearity).

Environmental variables	Sources	Abbreviations	Percentage contribution	
			Rhizophora apiculata	*Rhizophora mucronata*
Annual Mean Temperature	WorldClim-Global climate Data https://www.worldclim.org/	bio 1	20.8	10.2
Mean Diurnal Range		bio 2	62.4	43.8
Mean Temperature of Wettest Quarter		bio 8	6.9	4.4
Mean Temperature of Coldest Quarter		bio 11	6.9	17.5
Precipitation of Driest Month		bio 14	3.6	–
Precipitation of Driest Quarter		bio 17	–	2.7
Precipitation of Warmest Quarter		bio 18	3.1	2.3
Precipitation of Coldest Quarter		bio 19	2	2
Bulk density		BD	8.2	–
Total nitrogen		TN	8.4	2.9
Altitude		Alt	–	17.9

Table 2
Ensemble model performance of the targeted species.

Species	AUC	TSS	Sensitivity (model correctly predicting the presence of species)	Specificity (model correctly predicting the absence of species)
R. apiculata	0.99	0.967	1.0	0.967
R. mucronata	1.0	1.0	1.0	1.0

and Karnataka coast (0.49%) under RCP2.6–2050 and 2070 scenario accounting to ~ 868 km^2 and ~ 565 km^2, respectively. In contrast, based on the current climatic scenario, the predicted area for *R. mucronata* remains unchanged under RCP2.6–2050 and 2070 scenario. The overall decrease in extremely habitat suitability is estimated to be 0.41% and 0.43% under RCP2.6–2050 and 2070, respectively (Fig. 7a,b).

Under the RCP8.5–2050 climatic scenario, the ensemble model predicted gains in suitable habitat area for *R. apiculata* by about 33,815km^2in Sundarban delta (11.69%), Mahanadi delta and Chilika Lagoon (2.41%), Coringa mangrove (1.48%), Pichavaram and Muthupet (2.02%), Kerala coast (9.33%) and Udupi region (Karnataka coast, 0.40%) by 2050 (Fig. 6a,b). The increase in the habitat suitability predicted to be almost same under 2070 scenario except Sundarban delta (14.33%) and Mahanadi delta and Chilika Lagoon (3.70%). The model forecasts an overall increase in the habitat suitability for *R. apiculata* along the Indian coastline. However, in *R. mucronata*, the loss of suitable habitat is predicted in regions namely Pichavaram and Muthupet (0.82%), Kerala coast (2.77%), Mahanadi delta and Chilika Lagoon (0.08%) and Karnataka coast (0.56%) under RCP8.5–2050 and 2070. The overall suitable habitat is forecasted to decrease for *R. mucronata* under RCP8.5 scenario in the Indian subcontinent (Fig. 7a,b).

3.2. Contribution of environmental variables

The VIF analysis suggested that 9 variables each can potentially influence the distribution of both *R. apiculata* and *R. mucronata* in the Indian subcontinent. Six bioclimatic variables namely annual mean temperature (bio 1), mean diurnal range (bio 2), mean temperature of wettest quarter (bio 8), mean temperature of coldest quarter (bio 11), precipitation of warmest quarter (bio 18) and precipitation of coldest quarter (bio 19) are common for both the species. Precipitation of driest month (bio 14) and precipitation for driest quarter (bio 17) can also influence the distribution of *R. apiculata* and *R. mucronata*, respectively. In addition to climate, two soil parameters such as BD (bulk density of the fine earth fraction) and TN (total nitrogen) impacted the distribution of *R. apiculata* whereas for *R. mucronata*. Total Nitrogen in sediment and one topographic parameter i.e. altitude contributed the most to the distribution. Based on both correlation and AUC metric, assessment of the average variable importance (average of eight algorithms) revealed that bio 2 and bio 1 contributed maximum to the distribution for *R. apiculata*. Similarly, bio 2 and altitude are the major factors controlling the distribution of *R. mucronata*.

3.3. Core distributional shifts

Along the West Bengal coastline, the centroid for current habitat for *R. apiculata* is located at Kakdwip region. Later, the centroid of suitable habitat would shift towards Diamond Harbour region under future climate scenario (Table 3). The centroid of past (Mid-Holocene) distribution for *R. apiculata* was also located at Diamond Harbour region (Fig. 4a,b). Similarly, the centroid for *R. mucronata* distribution in current and future climatic conditions is located towards the south of Diamond Harbour region. Under past climate scenario the centroid was positioned at Diamond Harbour region (Fig. 5a,b).

Along Odisha coastline, the centroid for current habitat *R. apiculata* was positioned at Jagatsinghpur region. The centroid of future suitable habitat under RCP2.6–2050 and 2070 would be located at the same region as in current scenario. Under RCP8.5–2050 and 2070 scenario, the centroid will shift to Kendrapara region. The core of *R. apiculata* distribution during middle Holocene was located at Jagatsinghpur region (Fig. 4 a,b). Likewise, for *R. mucronata* the centroid was located at Puri region under past and current climate scenario. It will remain at the same position under RCP2.6–2050 and 2070 scenario but would shift towards Chilika under RCP8.5–2050 and 2070 (Fig. 5 a,b).

In Andhra Pradesh coastal regions, the centroid of current suitable habitat area for *R. apiculata* is in Kottapeta region whereas for future suitable habitat it will move towards Narsapur region under RCP2.6–2050, 2070 and RCP8.5–2050, 2070 scenario. The centroid for past climate scenario for *R. apiculata* was situated in the Bay of Bengal (Fig. 4a,b). For *R. mucronata*, the current and future suitable habitat centre under RCP2.6–2050 and 2070 scenario, would be positioned at East Godavari region. Later, the centroid for *R. mucronata* shifted to Visakhapatnam coast under RCP-8.5–2.50 and then to Srikakulam coast under RCP8.5–2070. The centroid for past suitable habitat area was situated at West Godavari region (Fig. 5a,b).

Along Tamil Nadu coast the centroid for past and current suitable habitat of *R. apiculata* was positioned at Manargudi region. However, the future suitable habitat area centre will shift to Pattukkottai region under RCP2.6–2050 and 2070 scenario. Under RCP8.5–2050 and 2070 scenario, the centroid would again shift back to Manargudi region (Fig. 4a, b). Similarly, the distribution core of past suitable habitat for *R. mucronata* was located at Thanjavur region. Later, it shifted to Nagapattinum coast in current climatic conditions. Then, the future suitable habitat would shift towards Kancheepuram region under RCP2.6–2050 and RCP2.6–2070 scenario. Under RCP8.5–2050 and 2070 scenario, the model predicts a complete loss in the suitable habitat for *R. mucronata* (Fig. 5a,b).

Along the Kerala coast, the centroid for current suitable habitat of *R. apiculata* is located at Kodungallur region. Further, the centroid for future suitable habitat will shift towards Trichur region under both RCP2.6 and 8.5, 2050 and 2070 scenario. The distribution core for

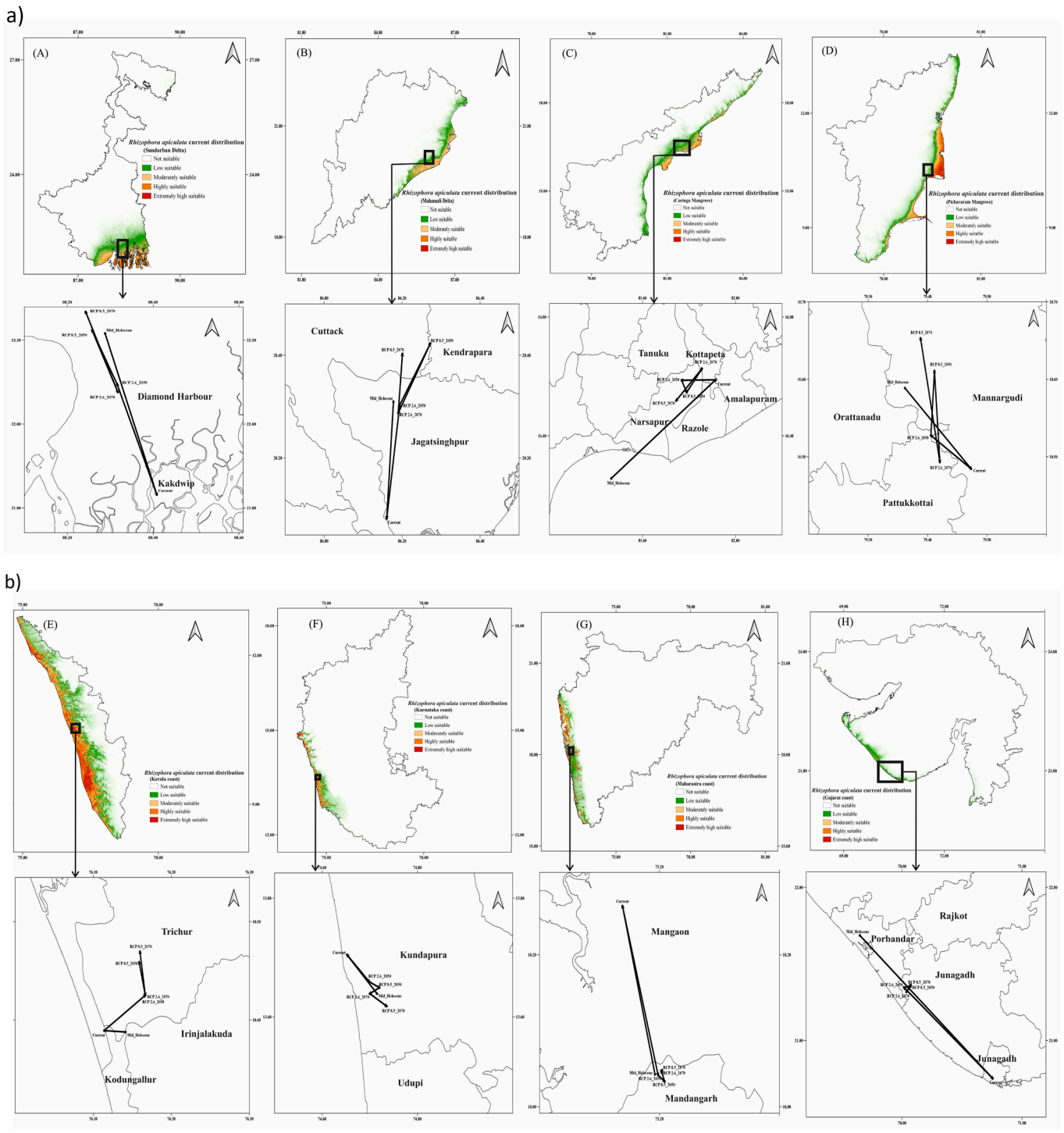


Fig. 4. Predicted current distribution and core distributional shift for *Rhizophora apiculata* **(a)** along the east coast and **(b)** along the west coast of the Indian subcontinent.

R. apiculata for past climatic scenario was positioned at Irinjalakuda region (Fig. 4a,b), which shifted to Malappuram coast as the current suitable area for *R. mucronata.* Then, the centroid would shift towards Kasargod region under RCP2.6–2050 and 2070 scenario while under extreme global warming condition it will shift towards Kannur region during 2050 s then towards Wayanad region in 2070 s (Fig. 5a, b).

The centroid shift for *R. apiculata* from current to future habitat suitable area in the state of Karnataka was not so prominent. The core of the distribution for past, current and future habitat suitable area situated at Kundapura region (Fig. 4a,b). However, the centroid for *R. mucronata* shifted broadly in the Karnataka state. During the past and current climatic conditions, habitat suitable area for *R. mucronata* has been located at Udupi region. The centroid for future habitat suitable area will move to Uttar Kannada region under RCP2.6–2050 and 2070 scenario and would further move to Kodagu region under RCP8.5–2050 and 2070 scenario (Fig. 5a,b).

In Maharashtra state, the centre for *R. apiculata* distribution under past climate scenario was located at Mandangarh region whereas during present condition the core habitat suitable area is located in Mangaon region. Later, the centroid for future habitat suitable area will again shift

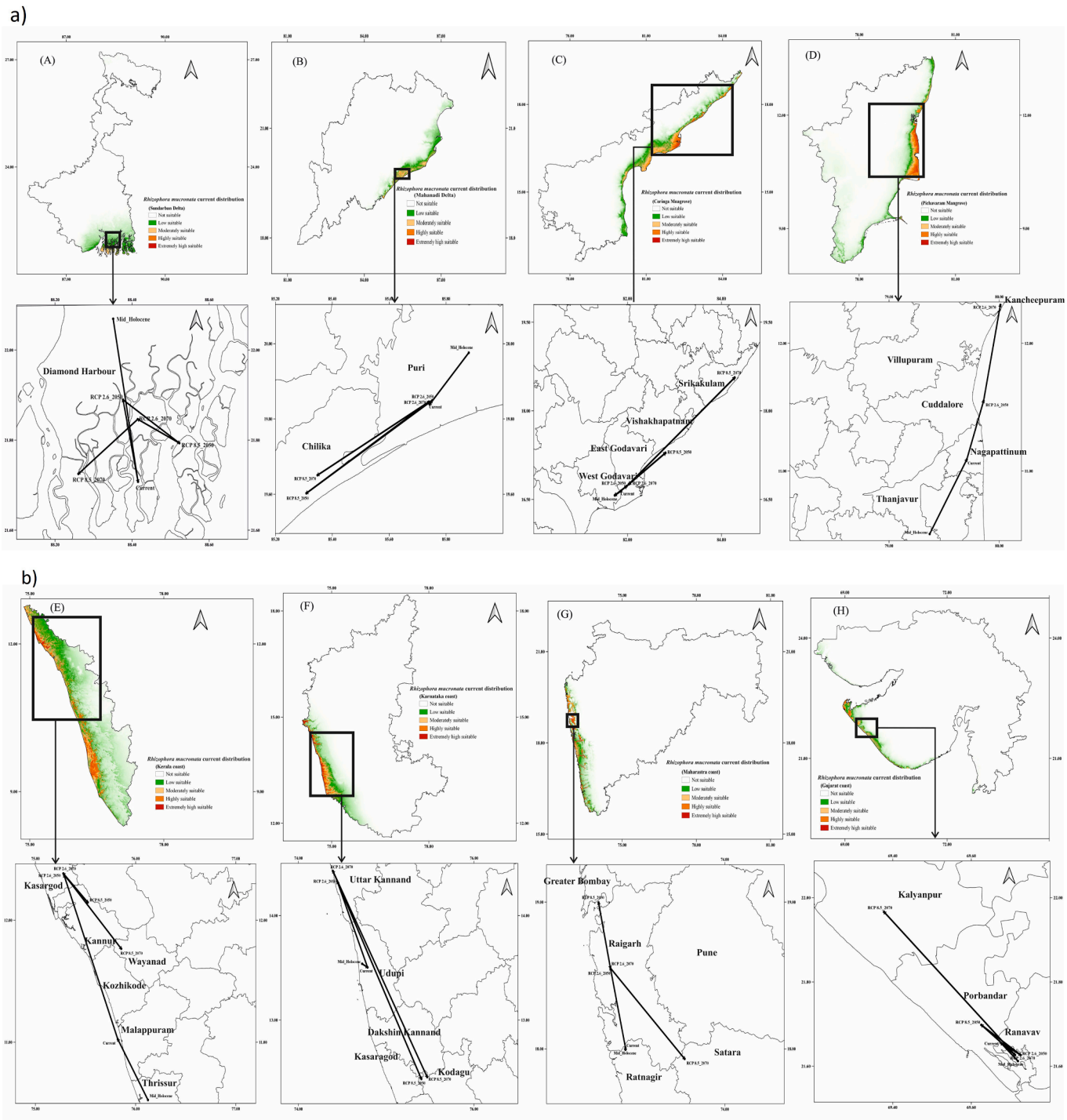


Fig. 5. Predicted current distribution and core distributional shift for *Rhizophora mucronata* **(a)** along the east coast and **(b)** along the west coast of the Indian subcontinent.

towards Mandangarh region under both RCP2.6 and-2050 and 2070 scenario (Fig. 4a,b). The core of *R. mucronata* distribution for the past and current climatic conditions was located at Ratnagiri region. However, it will shift towards Raigarh region under RCP2.6–2050 and RCP2.6–2070 scenario. On the other hand, the centroid for future habitat suitable area would move to Greater Bombay under highest global warming scenario in 2050 (RCP8.5–2050) and after that will shift to Satara under RCP8.5–2070 scenario (Fig. 5a,b).

In the state of Gujarat, the centroid for *R. apiculata* for past habitat suitable area was located at Porbandar which shifted to current suitable habitat was shifted to Junagadh region. Later, the centroids of future habitat suitable area was positioned at Junagadh region under both RCP2.6 and 8.5–2050 and 2070 scenario (Fig. 4a,b). Similarly, the centroid for *R. mucronata* for the past, current and future (under RCP2.6–2050 and 2070 scenario) habitat suitable area will remain at Ranavav region. However, under future extreme global warming conditions in 2050 (RCP8.5–2050) it will move towards Porbandar and would further shift to Kalyanpur region under RCP8.5–2070 scenario (Fig. 5a, b).

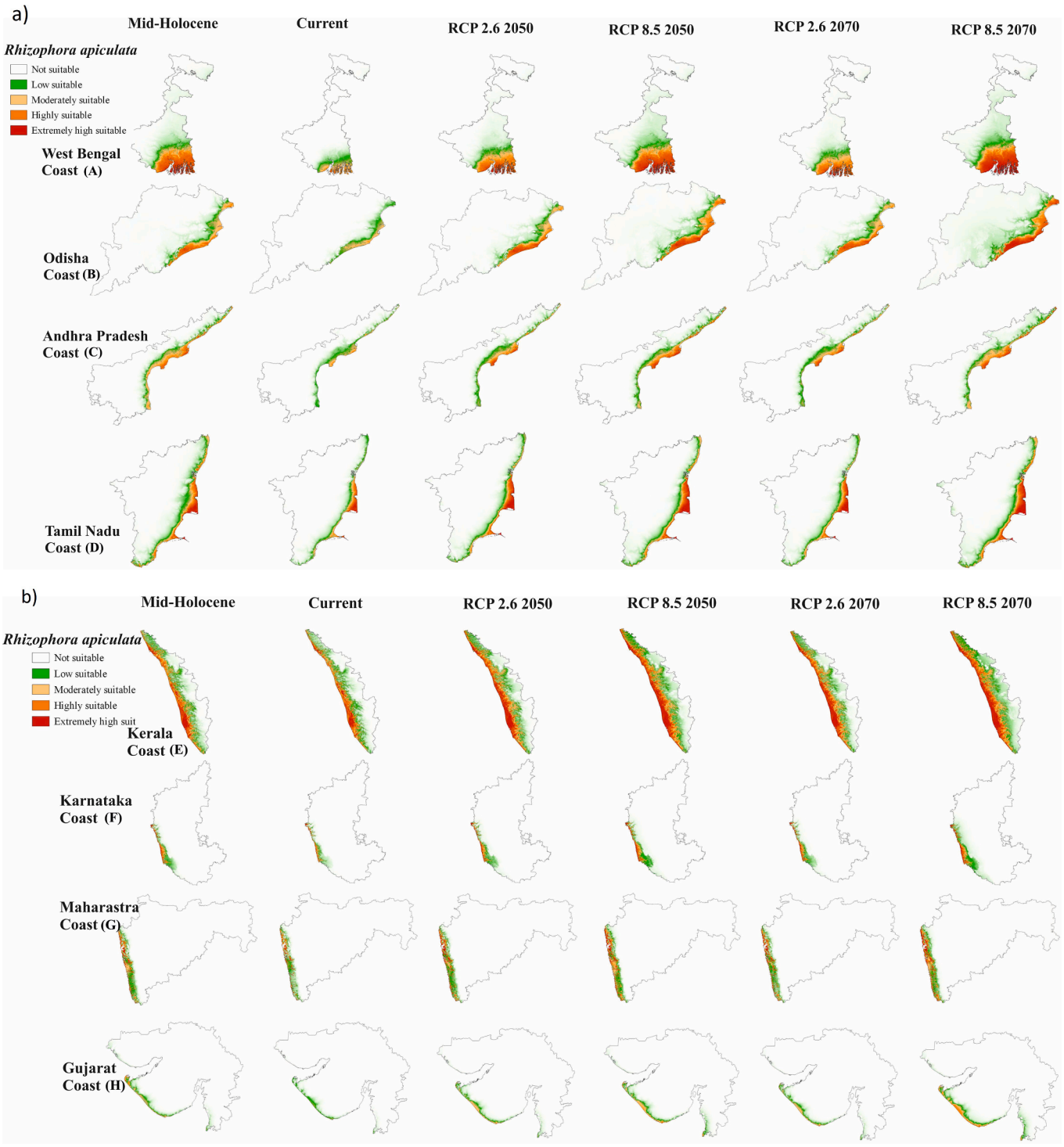


Fig. 6. Predicted past, present and future distribution for *Rhizophora apiculata* **(a)** along the east coast and **(b)** along the west coast of the Indian subcontinent.

4. Discussion

Each mangrove species' potential to survive in the changing climate is determined by its distinct physiological traits. Each mangrove species is predicted to react swiftly and decisively to climate changes like temperature, rainfall, and sea level rise/fall due to its specific tolerance level for each environmental component. Thus, we mapped the niche shift of two stilt mangrove species (*R. apiculata* and *R. mucronata*) along the Indian coastline across spatial and temporal scales.

4.1. Model prediction

Selecting a best suited single method to model every species is absolutely critical and unpredictable (Elith and Graham, 2009). Even though, the prediction of single model algorithm differs in accordance with the selected species, in this study, *maxent* is the best performed model based on evaluation metrics (AUC and TSS score). The *maxent* model is one of the most popular and effective models for analysing how species respond to environmental factors and how their distribution changes (Guisan and Thuiller, 2005), because it can render good

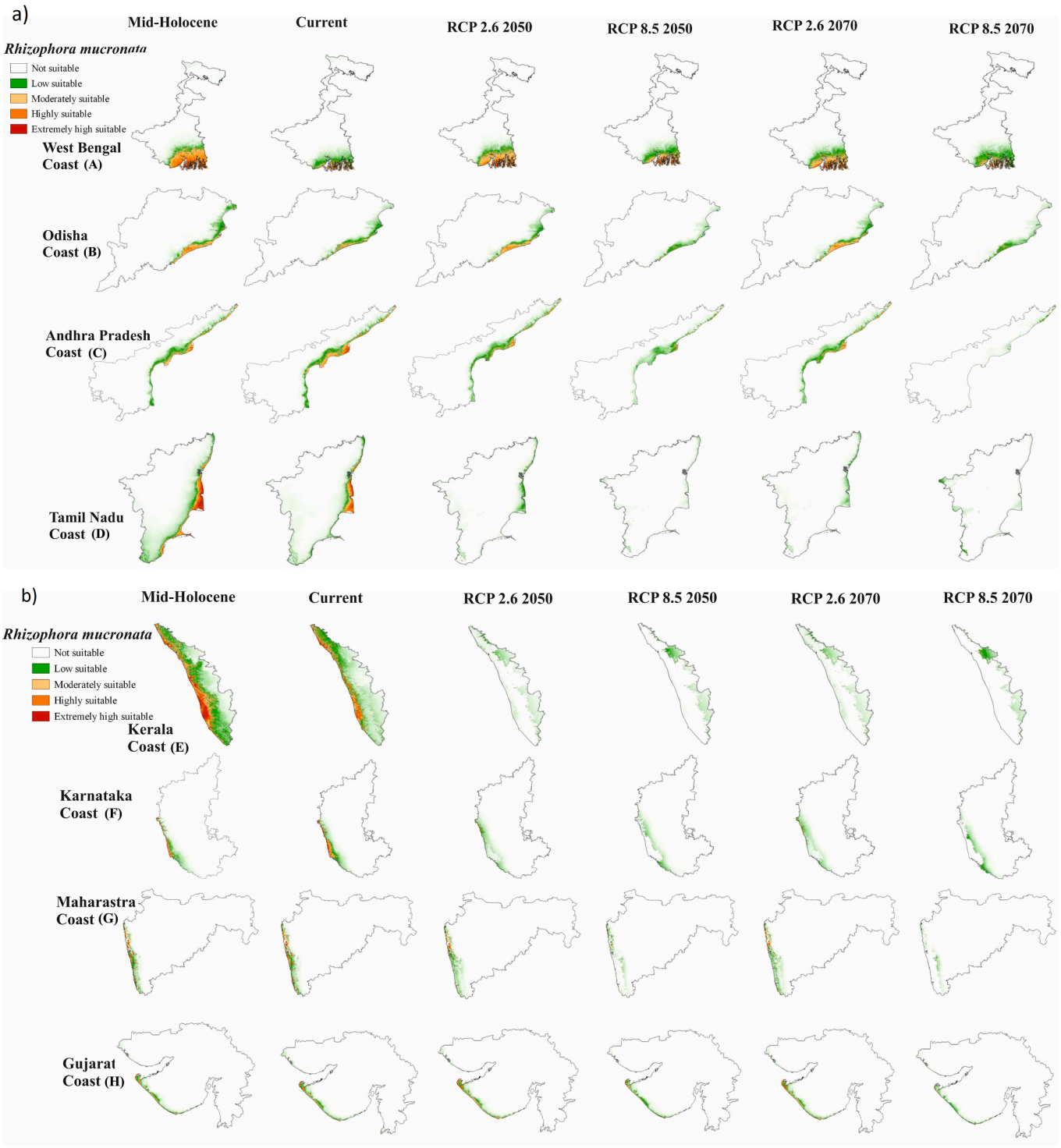


Fig. 7. Predicted past, present and future distribution for *Rhizophora mucronata* **(a)** along the east coast and **(b)** along the west coast of the Indian subcontinent.

performance even in small size in comparison to other single models (Elithet al., 2006; Phillips and Dudík, 2008). Several previous studies also reported the *maxent* as the best performed algorithm to model the potential distribution of various species (Hu et al., 2020; Dang et al., 2021; Radha and Khwarahm, 2022). The results of this study further support the validity of the ensemble modelling strategy over the use of a single model to project species distribution using the AUC and TSS evaluation methods (Thuiller et al., 2009; Shabani et al., 2016; Dong et al., 2020; Dang et al., 2021; Samal et al., 2022).

4.2. Climate and edaphic factors affecting the current distribution of Rhizophora species

The present study revealed that factors like precipitation, temperature and elevation strongly influenced the current distribution of both the targeted species, which was consistent with the pattern seen at both the worldwide (Simard et al., 2019) and regional scales (Banerjee et al., 2022). However, comparing the contribution of these environmental variables to the habitat distribution of the targeted species suggested that separate sets of environmental variables potentially affected the

Table 3
Potential niche shift locations for targeted mangrove species in response to climatic changes N.B: Distance of past and future centroids has been calculated with respect to current centroid point.

Species	Area	Centroid shifts									
		Past		Present	Future-2050				Future-2070			
		Mid-Holocene		Current	RCP2.6		RCP8.5		RCP2.6		RCP8.5	
		Coordinates	Distance (km)		Coordinates	Distance (km)	Coordinates	Distance (km)	Coordinates	Distance (km)	Coordinates	Distance (km)
R. apiculata	West Bengal	22.21°N, 88.29°E	50.80	22.65°N, 88.4°E	22.09°N, 88.31°E	62.80	22.22°N, 88.26°E	49.74	22.09°N, 88.31°E	62.79	22.07°N, 88.32°E	65.11
	Odisha	20.30°N, 86.17°E	25.20	20.08°N, 86.16°E	20.30°N, 86.19°E	24.75	20.42°N, 86.27°E	39.46	20.28°N, 86.19°E	22.52	20.40°N, 86.20°E	35.74
	Andhra Pradesh	16.25°N, 81.47°E	61.24	16.59°N, 81.92°E	16.59°N, 81.77°E	16.30	16.54°N, 81.80°E	13.86	16.52°N, 81.75°E	19.76	16.62°N, 81.86°E	7.02
	Tamil Nadu	10.58°N, 79.36°E	16.48	10.48°N, 79.47°E	10.52°N, 79.40°E	8.83	10.60°N, 79.41°E	14.82	10.48°N, 79.42°E	5.62	10.65°N, 79.38°E	21.16
	Kerala	10.38°N, 76.14°E	3.32	10.38°N, 76.11°E	10.42°N, 76.16°E	7.00	10.46°N, 76.16°E	10.44	10.42°N, 76.17°E	7.89	10.47°N, 76.16°E	11.38
	Karnataka	13.64°N, 74.71°E	9.27	13.70°N, 74.65°E	13.65°N, 74.69°E	7.01	13.64°N, 74.72°E	10.07	13.64°N, 74.70°E	8.55	13.61°N, 74.73°E	13.24
	Maharashtra	18.04°N, 73.19°E	25.24	18.26°N, 73.13°E	18.04°N, 73.19°E	25.24	18.03°N, 73.20°E	26.47	18.04°N, 73.20°E	25.36	18.04°N, 73.20°E	25.36
	Gujarat	21.68°N, 69.65°E	154.52	20.74°N, 70.75°E	21.33°N, 70.02°E	100.16	21.34°N, 70.07°E	97.34	21.31°N, 70.04°E	95.95	21.35°N, 70.08°E	96.54
R. mucronata	West Bengal	22.06°N, 88.35°E	40.58	21.70°N, 88.41°E	21.88°N, 88.37°E	20.43	21.79°N, 88.52°E	15.08	21.84°N, 88.41°E	15.24	21.72°N, 88.26°E	15.89
	Odisha	19.97°N, 85.88°E	21.02	19.83°N, 85.74°E	19.84°N, 85.75°E	1.57	19.59°N, 85.30°E	53.45	19.84°N, 85.73°E	1.56	19.65°N, 85.34°E	46.58
	Andhra Pradesh	16.57°N, 81.72°E	33.81	16.72°N, 81.97°E	16.72°N, 81.97°E	0	17.26°N, 82.81°E	107.12	16.76°N, 82.07°E	13.12	18.54°N, 84.29°E	320.82
	Tamil Nadu	10.49°N, 79.37°E	75.94	11.09°N, 79.70°E	11.53°N, 79.85°E	50.05	12.31°N, 80.00°E	138.39	Not suitable	-	Not suitable	-
	Kerala	10.51°N, 76.14°E	61.27	11.0°N, 75.83°E	12.36°N, 75.28°E	162.31	12.14°N, 75.52°E	130.12	12.38°N, 75.28°E	164.21	11.76°N, 75.85°E	83.73
	Karnataka	13.53°N, 74.73°E	6.91	13.49°N, 74.79°E	14.31°N, 74.45°E	97.37	12.42°N, 75.41°E	136.37	14.41°N, 74.40°E	113.04	12.43°N, 75.48°E	140.10
	Maharashtra	17.99°N, 73.16°E	1.13	18.00°N, 73.16°E	18.54°N, 73.04°E	60.79	18.99°N, 72.93°E	112.26	18.99°N, 72.94°E	111.94	17.92°N, 73.67°E	54.81
	Gujarat	21.61°N, 69.71°E	6.12	21.65°N, 69.67°E	21.62°N, 69.72°E	6.22	21.69°N, 69.62°E	6.80	21.62°N, 69.71°E	5.32	21.95°N, 69.39°E	44.19

habitat distribution of these two *Rhizophora* species along the Indian coastal regions.

Temperature was identified as the key factor followed by precipitation for driving the mangrove distribution. One of the temperature related variables i.e. bio 2 contributed the most to the habitat distribution of these two mangrove species. Our finding is confirming to the conclusion drawn from the study on physiology of mangrove ecosystems (Lin et al., 1994). Additionally, growth and reproduction of mangroves are highly controlled by temperature. Stomatal conductance and evapotranspiration are influenced by the temperature of the air and its impact on relative humidity, whereas sea surface temperature (SST) controls the metabolism and root growth of the aboveground plant through tidal inundations (Robertson and Alongi, 1992; Quisthoudt et al., 2012). Hong et al., (2020) reported that, the fruit of each tree of some of the mangrove species increases with latitudinal decrease, and a rise in temperature increases the survival rate of seedlings (Gillis et al., 2019). A study on the biodiversity of mangroves found that species richness and the composition of mangrove spatial assemblages are constrained by the winter temperature (Wu et al., 2018). For the Indo-West Pacific region, the recorded mean annual temperature was 20°–30 °C, mean maximum temperature of hottest month was 23°–38 °C, average minimum temperature of the coldest month was 13°–18 °C and minimum temperature tolerated was 10 °C (Duke, 2006). Thus, the models' predictions of the best ranges for environmental variables mainly agreed with the results of the field experiments. Our findings are consistent with numerous previous studies that reported temperature as a key driving force for the potential distribution of mangroves (Wu et al., 2018; Hu et al., 2020; Dang et al., 2021).

Additionally, the present study also revealed altitude as a significant factor for the distribution of *R. mucronata*. The elevation has frequently been identified as the significant variable for the distribution of mangrove species because it is well-associated with the tidal fluctuations and its amplitude, one of the important environmental parameters for the zonation of mangrove species along the coastline (Leong et al., 2018; Banerjee et al., 2021). Moreover, *R. mucronata* usually occurs at a regular freshwater input zone fringing along the estuarine channels towards the landward edges where the slope is higher. Our findings further revealed that bulk density of soil can also be a potential driver for the distribution of these mangrove species because higher bulk density of soil can help to increase the root diameter and biomass which in turn increases mangrove productivity (Ola et al., 2018, 2019). Our result is consistent with the previous study on restoration of mangrove in the Indo-Pacific region (Banerjee et al., 2021). The growth of these mangrove species have been found to be most likely restricted by the nutrients such as nitrogen. Due in part to the anoxic soil properties, ammonium is the main compound of nitrogen in mangrove soils, and ammonium uptake primarily supports tree development (Reef et al., 2010; Ray et al., 2014; Reis et al., 2017). In the present study, total nitrogen of soil is also detected as an influencing factor that can affect the distribution of these mangrove species in the coastal ecosystem.

4.3. Niche shift in response to future climate change scenarios

Coastal vegetation has been identified as being more affected by climate change, which might indicate either a niche range contraction i.e. loss of suitable habitat or a range expansion/shift i.e. migration of species towards inland. We precisely analysed the species-specific responses to projected climatic changes and the pattern of their niche range shifts. The hypothesis of niche contraction under future climate scenario postulated by Ellison (1994) was found to be valid for *R. mucronata* whereas, we found a landward shift of the suitable habitat under future climate scenarios for *R. apiculata*. It has been observed in the present study that the centroid of the future suitable habitat for *R. apiculata* is showing a northward shift along both east and west coast of India (except Karnataka and Maharashtra coast). The centroid of the future habitats for *R. mucronata* also showed a northward shift along the coastal regions (except Sundarban Delta, Mahanadi delta and Karnataka coast) but the suitable habitat for *R. mucronata* is predicted to decrease under future climatic conditions (Samal et al., 2022). As the sea level rises, the mangrove community relocates inland but are restricted to heights between mean sea level and peak tides (Duke, 2006). Mangroves have a limited range of ideal temperature conditions, therefore when temperature rises, their potential niche will shift north or south to locations with a conducive climate condition for their survival, and they will recede from locations that are unsuitable for their growth and survival. The suitable habitat loss in case of *R. mucronata* under future climate scenarios is mainly due to rise in temperature all over the Indian subcontinent. For the period of 2081–2100 compared to 1850–1900, the anticipated rise in temperature is by 1.0 °C to 1.8 °C in the low CO_2 emission scenario and 3.3 °C to 5.7 °C in the high CO_2 emission scenario (Arias et al., 2021). Based on the IPCC, AIR5 report, the future rise in global mean sea level is projected as 0.43 m under RCP2.6 and up to 0.84 m under RCP8.5 scenario by 21st century (Stocker et al., 2013). In accordance with this, the mangrove community will also shift as each mangrove species need specific saline water condition for its growth. Subsequently, *R. apiculata* commonly occurs in the mid-lower estuary and embayments where they can get sufficient tidal inundation to grow, whereas, *R. mucronata* preferably grows in areas subjected to regular freshwater inputs (Duke, 2006). Thus, increase in the area of highly suitable habitat for *R. apiculata*, and significant reduction for *R. mucronata* in the present study confirms the impact of climate change and sea level rise on the coastal ecosystem along the Indian coastline.

During Middle Holocene, there was moderate temperature and precipitation conditions which encouraged the mangrove species to expand their ranges to their largest extent. Based on past distribution projections, the highly suitable habitat for both *R. apiculata* and *R. mucronata* was found to occur in Sundarbans delta, Pichavaram mangroves and along the Kerala coastal regions of the Indian subcontinent during 6000 yrs BP. The location of centroid points of niche range for both the species shifted mostly towards the north and landward from mid-Holocene to the current time suggesting a higher sea-level specifically in these sectors of the Indian coastline. These results agree with Cannon et al., (2009), which noted that during the deglaciation, coastal mangroves and swamp forests experienced total biogeographic replacement. The predicted maps for both the species under the past (Middle Holocene) are complementing many previous studies based on fossil pollen records and reveals wide distribution of both the *Rhizophora* species along the east coast during the Middle Holocene time period (Figs. 8 and 9) (Farooqui and Vaz, 2000; Bhattacharyya et al., 2013; Hait and Behling, 2019; Srivastava and Farooqui, 2017) and west coast of India (Limaye and Kumaran, 2012; Limaye et al., 2014; Alappat et al., 2021).

Subsequently, the relative sea level changes may also have a potential impact on the distribution of these species because salinity acts as a primary factor for the zonation and growth of these species. Studies on Middle Holocene Sea level changes show a + 5 m rise for 6000 years BP (Nageswara Rao and Sadakata, 1993), +3 m rise around 7300 years BP (Banerjee, 2000) along the east coast of India and + 1.5 m rise around 8000–7000 years BP (Alappat et al., 2021) along the west coast of India. Consequently, the salinity gradient is also optimum because of moderate precipitation and temperature conditions throughout the year along with arise in sea level, which encourages the growth of stilt mangroves like *Rhizophora* species.

4.4. Limitations of the study

The future projections in this study are only based on climate data for future scenarios although there are several other physicochemical and environmental factors which influence the distribution and growth of coastal vegetation. Hence, it is crucial to add such variables also while projecting the future distribution of species. Presently, such data are available only for current climatic conditions and that also in a broad

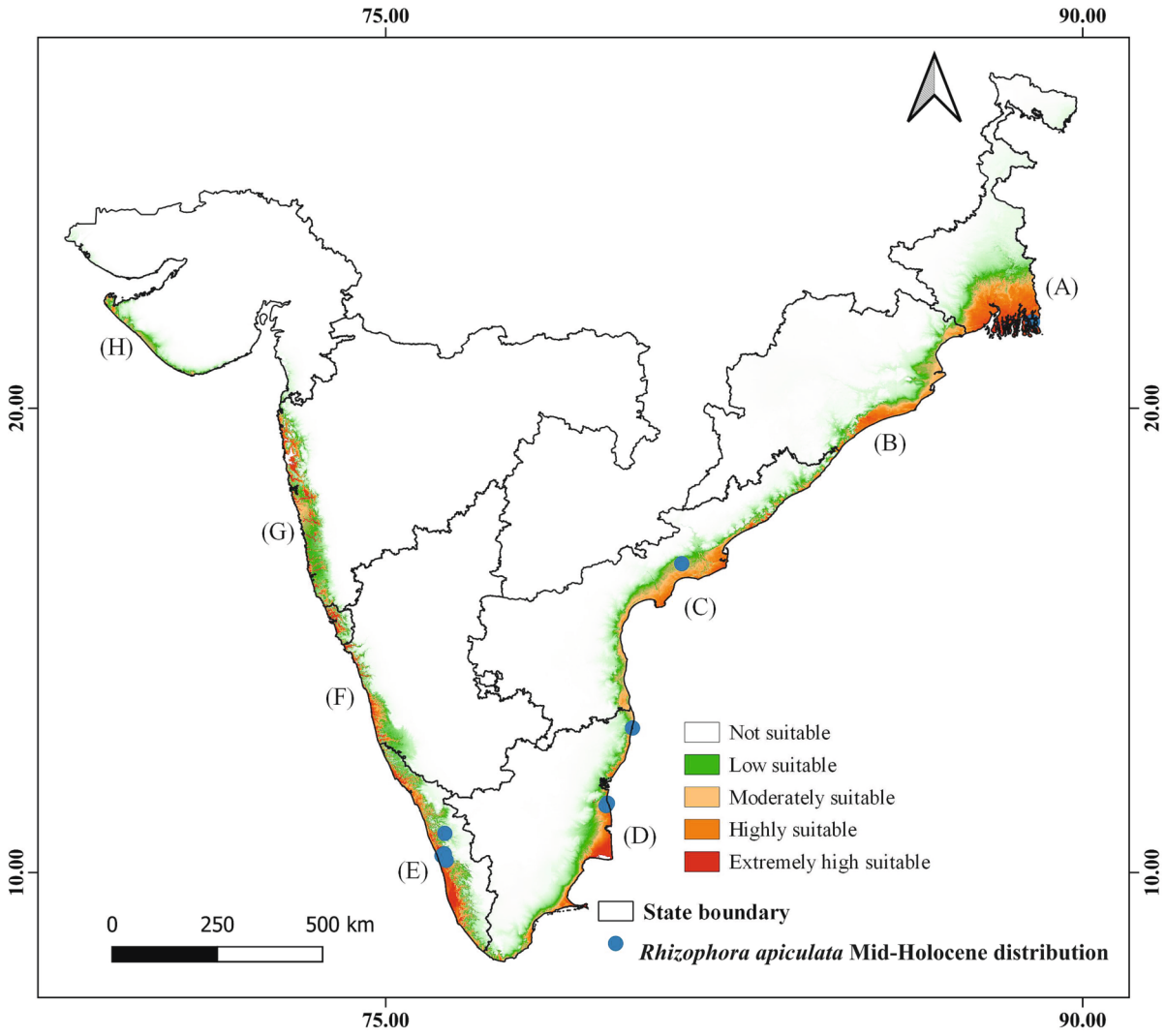


Fig. 8. Mid-Holocene fossil pollen records of *Rhizophora apiculata*.

spatiotemporal scale. Therefore, it is crucial to develop finer resolution environmental and edaphic variables for future climatic scenarios to provide more robust future projections for species niche shift and habitat suitability. Additionally, other potential driving forces which influence the distribution of the mangrove species includes the coastal geomorphological features which might have been a limiting factor causing mass loss or restricting mangroves in narrow fringes as they shift landward due to rising sea levels (Asbridge et al., 2015).Genetic analyses, controlled experiments, and the data availability on these species' basic habitats from fossil records may further increase the accuracy of the prediction models. Since environmental conditions can fluctuate at a smaller scale, particularly in estuarine and coastal ecosystem, modelling at various spatial and temporal scales and including climate proxy data from direct observations can further improve the predictive accuracy. However, by giving these errors equal weight, the threshold used in this study TSS minimizes the total commission and omission errors. An evaluation criterion that prioritises sensitivity over specificity may also be preferred but this would also produce significant commission errors (Das et al., 2019).

4.5. *Future priority conservation areas (PCAs) along the Indian coastline*

Future loss of habitats with significant loss in species richness highlights the necessity to preserve habitats that are environmentally suited for the selected species. The areas that are presently suitable for these species and will continue to be favourable even in future climatic conditions should receive the highest priority for restoration and conservation plans. Other studies have also investigated the potential distribution of endemic species for the implication of conservation strategies globally (Radha and Khwarahm, 2022; Hama and Khwarahm, 2023). The coastal regions are one of the densely populated areas with numerous developmental activities causing to freshwater restrictions, environmental pollution and encroachment along the coasts. Consequently, to achieve efficient coastal management and restoration planning we should integrate the anthropogenic aspect in the framework of the conservation policies. Most prominently, the highly suitable habitats i.e., Sundarbans delta, Chilika lagoon, Mahanadi delta and Kerala coastline must be given high priority in addition to other sectors of the coastline for protection and conservation. Loss in species richness along the coastline will also increase the vulnerability of mangroves in response to future climatic conditions. It is important to note that by summing the binary rasters for each species, we were able to assess species richness as well as identify the priority conservation areas. Although this method has been employed frequently in multispecies modelling research (McKerrow et al., 2018), this does not take into account the biotic interactions (like competition and facilitation), which could cause an underestimation or overestimation of species richness. Thus, the biotic interconnections between species may be incorporated

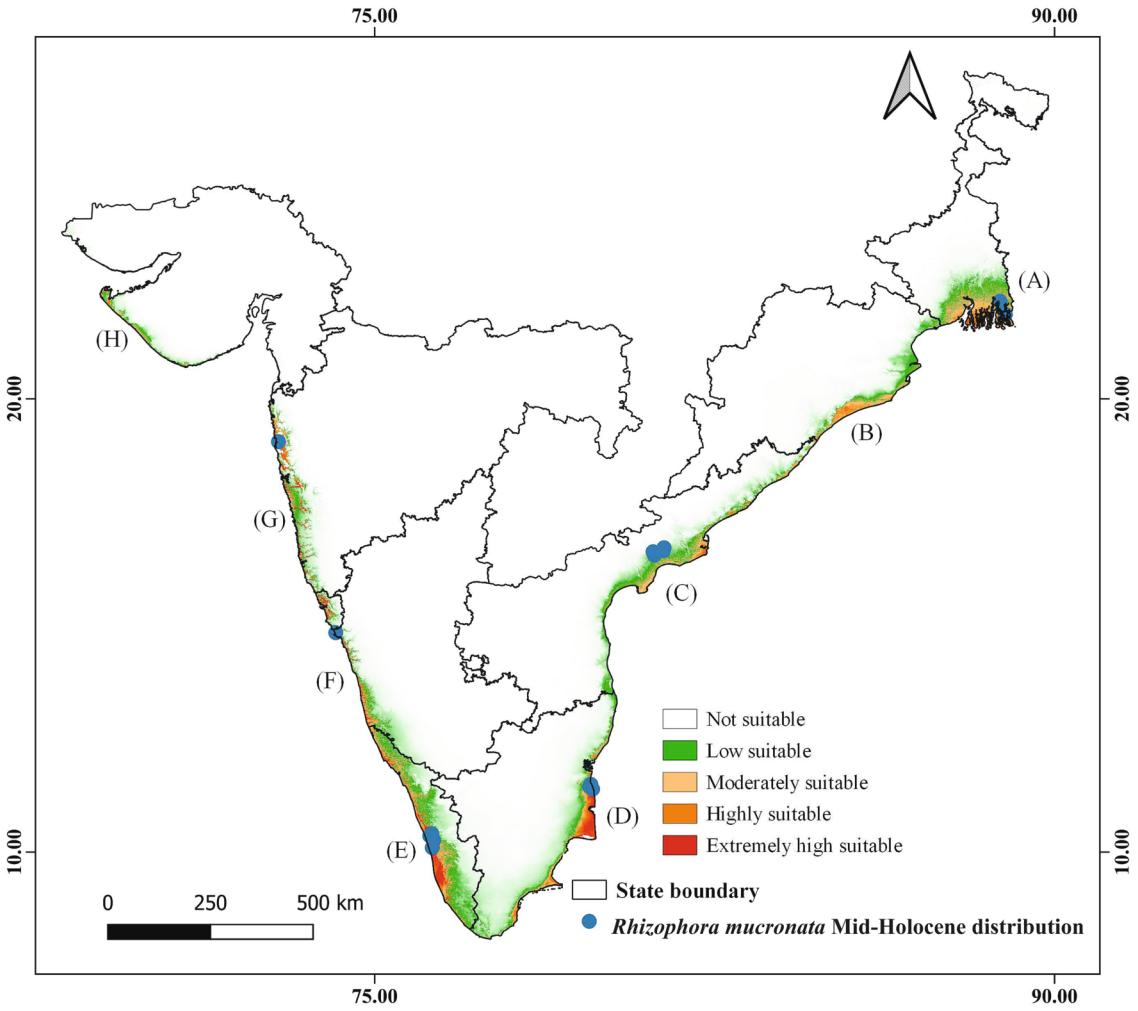


Fig. 9. Mid-Holocene fossil pollen records of *Rhizophora mucronata*.

into the more complicated community-level modelling method to further strengthen the conservation priority target areas determined by our simplified species-level modelling framework (Dormann et al., 2018).

5. Conclusions

Understanding mangroves' responses to changes in temperature, precipitation and sea level patterns over time and space requires an estimation of species-specific distributional ranges and shift along their habitats. In this study we mapped the shift in the spatial and temporal distribution of two stilt mangrove species (*R. apiculata, R. mucronata*) along the Indian coastline. It showed that temperature, precipitation, and elevation had an impact on both the targeted species' present distribution, which was consistent with the trend seen at both the global and regional scales. Mean diurnal range of temperature is identified as the key factor followed by precipitation, bulk density of soil and total nitrogen in mangrove sediments which are driving the species' distribution. However, surface elevation also played a significant role in the distributional shift of *R. mucronata*. The centre for suitable habitat for *R. apiculata* along east and west coast of India under future climate change scenarios would be shifting northwards except along Karnataka and Maharashtra coast while for *R. mucronata* the core distributional shift would also be towards north except along West Bengal, Odisha and Karnataka coast. Habitat suitability for both the species shifted towards north and landward from mid-Holocene to the current time suggesting a rise in the sea-level along different sectors of the coastline. Finally, this study suggests the highly suitable habitats along West Bengal, Odisha and Kerala coast as the priority conservation areas (PCAs) in addition to other sectors of the coastline for mangrove protection and conservation. Emphasis should also be given to the loss in species richness which will also increase the vulnerability of mangroves in response to future climatic conditions. Hence, the priority conservation targets established by this streamlined species-level modelling method can be strengthened if the complex community-level modelling framework incorporates the biotic relationships between species, coastal geomorphological features as well as by generating finer resolution environmental and edaphic variables for future climatic scenarios.

CRediT authorship contribution statement

Pujarini Samal: Investigation, Data curation, Formal analysis, Writing – original draft, Validation. **Jyoti Srivastava:** Supervision, Resources, Conceptualization, Writing – review & editing. **Bipin Charles:** Resources, Methodology, Software, Writing – review & editing. **S.R. Singarasubramanian:** Data curation, Formal analysis.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Pujarini Samal reports financial support was provided by India Ministry of Science & Technology Department of Science and Technology.

Data availability

Data will be made available on request.

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