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Improving spatial transferability of ecological niche model of *Hevea brasiliensis* using pooled occurrences of introduced ranges in two biogeographic regions of India

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ABSTRACT

Improved spatial transferability of ecological niche models is crucial for accurately predicting species preferred habitat; this is especially true for a planted tree species (*Hevea brasiliensis* Muell. Arg.). Amazonian valley of South America (AZ) is known as native range of this species. To test the transferability of Maxent ecological niche model among two distinct bio-geographical regions of India, Western Ghats (WG) and North-East (NE) regions and AZ, the present study was designed. The present spatial distribution of *H. brasiliensis* was evaluated using the Maxent algorithm using bioclimatic variables and species occurrence data from respective regions. An alternate approach of calibrating the model with pooled occurrence points of various introduced ranges of the species was adapted for predicting the species' presence in unsampled region.

Spatial distribution of *Hevea* species in two biogeographic regions of India modelled by Maxent was found to be quite accurate when the model was calibrated with the sampled occurrence points of the same region as evidenced from our previous studies. However, the present study addresses the issue related to transferability of niche based model to predict the probable distribution of *Hevea* species in an unsampled region based on either its native or introduced range of the species. The result indicates that transferability depends on the extent of similarity between the climatic spaces occupied by the species in sampled region and unsampled regions of the species' distribution. The spatial transferability of the model was improved by using pooled occurrence data of the species from both introduced regions.

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1. Introduction

Predicting the potential ecological niche of a species in an unsampled geographical space based on existing distribution is of immense importance in ecosystem management applications (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). Several algorithms were used in ecological niche models (ENMs) in recent years for predicting the species distribution based on availability of input data and the extent of the study area (Araujo and Guisan, 2006; Garcia et al., 2013). The geographical area maintaining equilibrium between species and environment represents the potential niche of that species. This geographical area can represent the part of the fundamental niche where the species actually exits at a given time (Elith and Leathwick, 2009; Soberón and Peterson, 2005).

Usually a species may occupy a subset of potential niche in a geographical space, which is called as realized niche (Hutchinson, 1957). There are several reasons for the failure of a species to occupy the entire potential niche such as dispersal limitation, intra-species competition, resource availability and certain spatial limitations (Mott, 2010). The geographical and ecological distribution of a species was linked to a framework called Biotic-Abiotic-Mobility (BAM) (Soberón and Nakamura, 2009). In BAM framework, it is understood that the relationship between the existing realized niche and species' ability to compete for occupying larger niche is altered by different drivers. The potential niche that is yet to be occupied by a particular species is called as unfilled niche for that species (Broennimann and Guisan, 2008). Identification of potential niche for future invasion of the species will help in understanding invasive behaviour of species (Pulliam, 2000). This is often regarded as one of the unsolved problems in species-environment relationship modelling (Seoane et al., 2005).

At the initial stage of the development of ENMs, the efficiency of these models for identifying species' niche was largely tested for the region in which these models were developed. Subsequently, it has

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become more relevant to calibrate the model for native range or existing introduced ranges of a species and projecting them to unsampled regions to identify potential geographical extent of species introduction. This is referred as transferability of the model (Randin et al., 2006). However, achieving the spatial transferability is difficult through usual modelling approaches. In most of the cases, species presence data either from native range or introduced range were used in niche based modelling approach for predicting species distribution (Fernández and Hamilton, 2015; Guisan and Thuiller, 2005; Randin et al., 2006). Species acquire wide range of environmental tolerance through hybridization, evolution of better competitive ability and interaction with other neighbouring species, which may lead to changes in realized niche of a species (Blossey and Notzold, 1995). An introduced range of a species represents the region where the interaction between the environmental conditions and the physiological requirement results in survival and growth of a particular species. But, it becomes challenging to model the future distribution of a species using ENMs, where the species is introduced to newer regions based on not only favourable climate but also anthropogenic pressure (Pulliam, 2000; Silvertown, 2004). Under those situations, application of ENM is more successful if the models are calibrated with occurrence points of introduced ranges where the species has occupied a changed climate space compared to its native range (Fernández and Hamilton, 2015).

Usually successful transferability of niche model was often limited due to incomplete dispersion processes, where the species is naturally introduced and therefore, full range of introduced ranges cannot be represented by the sampling procedure adopted (Beaumont et al., 2009). In other words, the primary assumption of successful application of ENM for predicting distributional potential of any species in unsampled region is the conservatism of the species niche across the space. If the species-environment relationship is conserved between two geographical regions, model transferability between those regions is expected to be higher (Mau-Crimmins et al., 2006). On the contrary, asymmetrical transferability may be observed in ENMs due to different range of predictor variables in training as well as test sites of the model (Randin et al., 2006). In addition to that, one of the major variables for accurate extrapolation of climate-species relationship is the appropriate sampling space used for model calibration (Albert et al., 2010; Fourcade et al., 2014; Lazo et al., 2016; Zhu et al., 2012).

Previous studies have demonstrated ENM generalization by calibrating the model for one region and projecting for other and vice-versa (Randin et al., 2006; Verbruggen et al., 2013; Zhu et al., 2012). Randin et al. (2006) have introduced an index to evaluate model transferability called as transferability index (TI) that ranges from 0 (least transferable) to 1 (highly transferable) considering the AUC values of model simulation between two regions taking one as training site and other as projected site and vice versa. Transferability often appears to be asymmetric in different species and ENMs. Improving the transferability remains more challenging in case of plant species than birds and butterflies due to unique dispersal mechanisms through anthropogenic agents, winds and runoff etc. and factors associated with plant propagation (Heikkinen et al., 2012; Whittingham et al., 2003). Although it is difficult to achieve transferability in ENMs with plants, this is found to be informative in terms of species characteristics and invasive behaviour (Broennimann and Guisan, 2008; Strubbe et al., 2013).

In the present study, *Hevea* has been considered as target species due to its increasing importance as a plantation crop in India. *Hevea* is a native species of Amazonian valley of Brazil. This species could not be established as a plantation species in its native range of Brazil due to a deadly epidemic of South American leaf blight disease (Dean, 1987). Being a native species of Amazonian valley of Brazil, it was introduced to tropical Asia in 1876 through Kew Garden in the UK with the seeds brought from Brazil (Hong, 1999; Wycherley, 1992). This species was brought by the English colonialists from Brazil and introduced to many countries in South and South East Asia, including India in the 1870s. In India, this species was grown in WG region since beginning in the 19th century and proved to be one of the most widely adapted and economically viable crops. Since 1960s, this species has been cultivated in NE region of India in order to extend its cultivation in newer regions for bridging the gap between the global demand and the production of natural rubber. *Hevea* species was initially established in WG particularly in the state of Kerala and Tamil Nadu, which can be referred to as early introduced range and the NE region can be referred to as recently introduced range of *Hevea* in India (Jacob and Raj, 2012). *Hevea* trees are grown as plantation crop in these two regions of India, where the plants are multiplied using a vegetative propagation technique and transported to the site of plantation. Therefore, socioeconomic and anthropogenic factors contribute to the dispersion pattern of the species (Ray et al., 2016). However, climate plays a major role in deciding the suitability of a region for *Hevea* tree plantations.

Application of ENM in predicting distribution of such species was initially a challenge for the researchers. Predicting the distribution of *Hevea*, which is controlled by multiple factors prominently by climate, using Maxent ENM was attempted in the present study to evaluate the spatial transferability of the model. Location specific species-environment relationships in different regions of India will reflect species' tolerance to environment. This relationship between species and environment within introduced ranges may influence the transferability of the ENMs of a particular species. On this background, we hypothesise that reciprocal transferability of the ENM between two introduced regions can be improved by considering both regions for model calibration. Therefore, the objectives of the study are (1) to assess the transferability of the model in predicting the present distribution of this unique species among its native range, Amazonian basin of South America (AZ), two introduced ranges in India (WG and NE), (2) to test the model transferability between introduced ranges in India by calibrating the model with pooled occurrence data of WG and Tripura state (early introduced range) and projecting to other parts of NE region; and, in reverse , calibrating with pooled occurrence data of NE region and Kerala state and projecting to the WG region under same geographic space, (3) to compare the realized niche characteristics of AZ, WG and NE regions.

2. Methods

2.1. Target species and its occurrences

The study focuses on *Hevea* species, one of the important cash crops in India that contributes around 0.2% towards GDP growth in India (Anuja et al., 2012). This tree belongs to the family Euphorbiaceae. It is sturdy and quick growing tree, which grows on wide variety of deep and well drained soils (Verheye, 1980). The latex, produced in the laticiferous vessels in the soft tissue of the bark, is normally oozed out through a slanted cut on the bark and collected in a container kept attached with the tree trunk. The rubber content present in the latex is chemically separated and is taken for further processing (Wycherley, 1992).

A total of 143 points of *Hevea* plantation in Kerala and 57 plantations in Tripura were taken for transferability studies. The geographic positions of those plantations (degree decimal units) were ascertained for sample locations in both states through field visits and with the help of Google-Earth images. Selection of sample points was done using 10 km × 10 km grid placed on the Google Earth image to avoid spatial autocorrelation as described by Veloz (2009). Moreover, the knowledge of field personnel from the Indian Rubber Board was also used to locate rubber tree plantations to avoid spatial bias (e.g., plantations along the road we travelled). While recording occurrence points, a patch of a plantation, covering 1–5 ha with comparable topography was recorded as a single point. However, more points were taken from larger estates occupying different topography within the same grid, which were representative of actual plantation distribution. The number of species occurrence points in WG and Tripura was 275 whereas the points in

NE region and Kerala were added to 270. In addition to that 82 points of *Hevea* plantations of Amazonian region of Brazil were taken from global portal for biodiversity facility (GBIF) (www.gbif.org) as native population (AZ) and used for niche similarity studies using ENMTools (Warren et al., 2010). The occurrence data collected from GBIF portal were subjected to data cleaning procedures as described by Chapman (2005). The data has been downloaded as KLM files as well as latitude and longitude (degree decimal) of occurrence points. The occurrence points (KLM file) were superimposed on Google Earth images to confirm positional correctness within study area. The occurrence points were converted into a point-shape file using Arc-GIS 2010 software and overlaid on the polygon of the study area and 10 km × 10 km grid to take care of autocorrelation among the points. The outliers and close-by or duplicated points were removed and the cleaned occurrence data set were finally used for calibrating the model.

2.2. Study area

The study area includes the native range of the species i.e., Brazil (the Amazonian basin of South America, AZ) and two *Hevea* growing regions in India i.e., WG and NE (Fig. 1). North and north-eastern parts of Brazil mainly represent the Amazonian basin region, which shows spatial and seasonal temperature homogeneity. The annual rainfall of the region varies from 2000 mm in central Amazon to 3000 mm in Northwest Amazon with 2800 mm in eastern part of Amazonian base (http://www.fao.org/ag/agp/agpc/doc/counprof/brazil/brazil.htm accessed in April 2016). The AZ, WG and NE regions fall under diverse world biodiversity hotspots show distinct biogeographic characteristics (Table 1). The WG and NE are two major biodiversity hotspot regions of India: WG is the mountain range running parallel to the western coast of Indian peninsula, whereas NE region is located in the Indo-Burma hotspot (Dean, 1987; Rodgers and Panwar, 1988; Mittermeier et al., 2011). The WG ecosystem is often disturbed by mining activities, whereas, shifting cultivation (*Jhumming*) causes similar disturbances in NE region resulting in degraded and unproductive land (INCCA, 2010). Due to extensive shifting cultivation by the natives in NE, the ecosystem has been degraded leading to unproductive lands for agricultural use (Jacob, 2000; Jiang and Wang, 2003; Krishnakumar and Meenattoor, 2003). However, *Hevea* plantation is found to be an alternative source of socio-economic support to the native community.

In WG, mean maximum temperature during the coldest months of December and January varies from 29 °C in some part of the peninsula to about 18 °C in the North, whereas the mean minimum temperature ranges from about 24 °C in the extreme South to below 5 °C in the North. The period of March to May is usually characterised by continuous and rapid rise of temperature. Rainfall recorded in different places of the zone ranged from 3000 to 6000 mm. *Hevea* is being cultivated in the coastal slope of WG for more than a century. The NE region of India receives annual rainfall of an average of 2450 mm. Precipitation in this region occurs due to mainly south-west monsoon during May–October. The temperature varies from 15 °C to 32 °C during summer and 2 °C to 26 °C during winter season (Sehgal et al., 1992). These two regions are the major *Hevea* growing areas in India with diverse local climatic, soil and socio-economic conditions. Considering this contrasting climate, WG and NE regions were taken as the study area.

2.3. Optimization of bioclimatic variables for better transferability

The nineteen bioclimatic variables with 30 s (ca 1 km) spatial resolution were subjected to multi-collinearity test by using Pearson correlation coefficient (r) using ENMTools software to examine the relationship among the variables. Most of the ENMs are typically based on the relationship between the species presence records and climate variables. The actual relationships may not reflect if the input climate variables are spatially correlated and therefore, many combinations of climate variables can explain the species niche distribution equally well. The climate variables with correlation of $r > \pm 0.7$ were excluded for simulating the model (Dormann et al., 2008). Out of 19 bioclimatic variables, 8 variables viz. mean diurnal range of temperature (Bio2), isothermality (Bio3), temperature seasonality (Bio4), minimum temperature during coldest month (Bio6), precipitation during driest month (Bio14), precipitation seasonality (Bio15), precipitation during driest quarter (Bio17) and Precipitation during coldest quarter

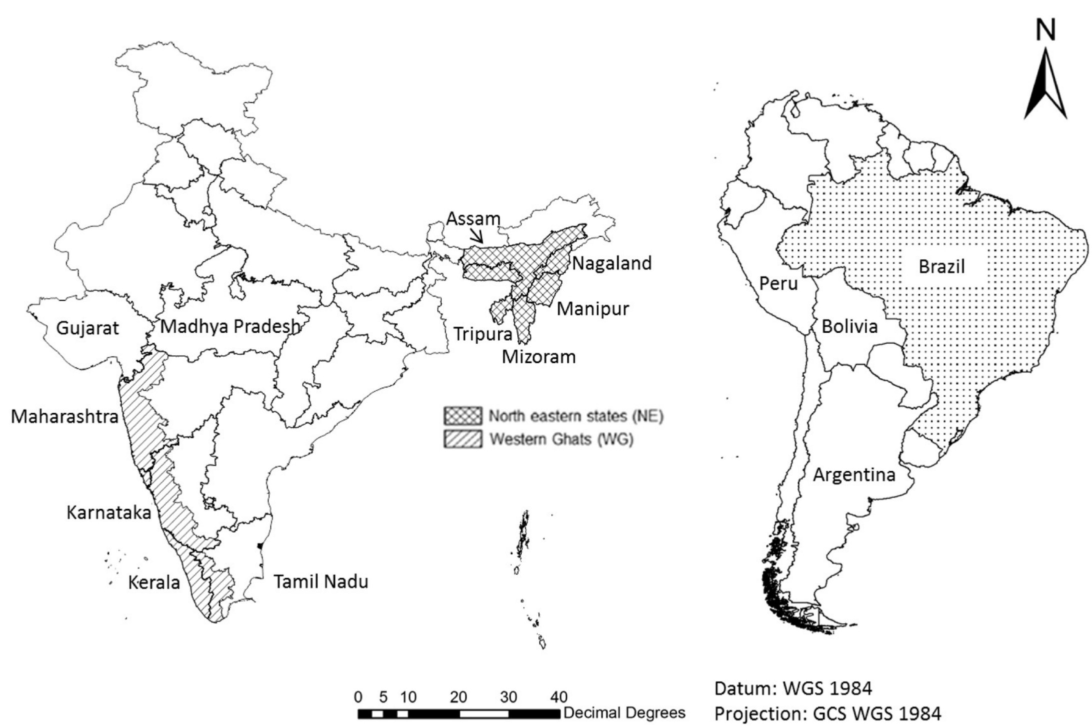

Fig. 1. Study area: Western Ghats (WG) and North Eastern region (NE) indicating the parts of Indian states under each region.

Table 1
Bio-geographical profile of study regions.

Characteristics	Amazonian basin region	Western Ghats region	North-eastern region
Agro-climatic zonation	North and north-east parts of Brazil, which is located in western hemisphere.	West coast plains and Ghats regions	Eastern Himalayan region
Climate based ecosystems	Climate varies from very humid and hot climate to very strong semi-arid climate.	Hot humid per humid eco-regions	Warm per humid eco-regions
Soil types	The major soils are extremely weathered i.e., Ferralsols.	Red, lateritic and alluvial derived soil	Red and lateritic soil
Annual rainfall	Northwest of Amazon receives average annual rainfall of > 3000 mm. This is mostly contributed by humid air brought by easterly winds.	2000–3200 mm (Mainly due to south-west Monsoon, 20% contributed by northeast monsoon)	1600–2600 mm (Mainly by south west monsoon)
Temperature	Annual average temperature of above 25 °C is observed in Amazonian basin region with maximum temperature of 40 °C in interior low lands of Northeast region.	Average annual temperature of Western Ghats region is 15 °C. Mean temperature ranges from 20 °C in south to 24 °C in north.	15 °C to 32 °C during summer, 2 °C to 26 °C during winter season

(Bio19) were selected as input variables to the model. The overall methodology followed to improve the model transferability is depicted in Fig. 2.

2.4. Ecological niche modelling

To map the potential niche distribution of *Hevea* species under both climatic scenarios of WG and NE, the most recently available Maxent 3.3.3k software was used (Phillips et al., 2006). Maxent is a machine learning algorithm that follows the principle of maximum entropy in which the software takes species presence only data and predicts the distribution of the species that is closest to uniform distribution. It maximises entropy within distributions that satisfies the constraints derived from species occurrence points. In our previous study, the Maxent model was employed to predict the distribution of *Hevea* species based on bioclimatic variables as predictive input, where model calibration and projection was done in same introduced regions (Ray et al., 2014). The parameters used in the Maxent model were justified based on previous studies (Elith et al., 2006; Fourcade et al., 2014).

In the present study, the model was calibrated in native range of the species and projected to other introduced range such as WG and NE. Then model predictability was also tested in one of the introduced ranges in India (NE) based on calibrating the model with occurrence points of native range (AZ) and another of the introduced range in India (WG) and poor spatial accuracy in predicting the actual distribution was observed (data not shown here). Therefore, the studies on model transferability was carried out by calibrating the model in either of the introduced ranges in India and projected on the other and vice-versa.

The experimental design was aimed to use only climate variables and by default, Maxent model determines the features types automatically

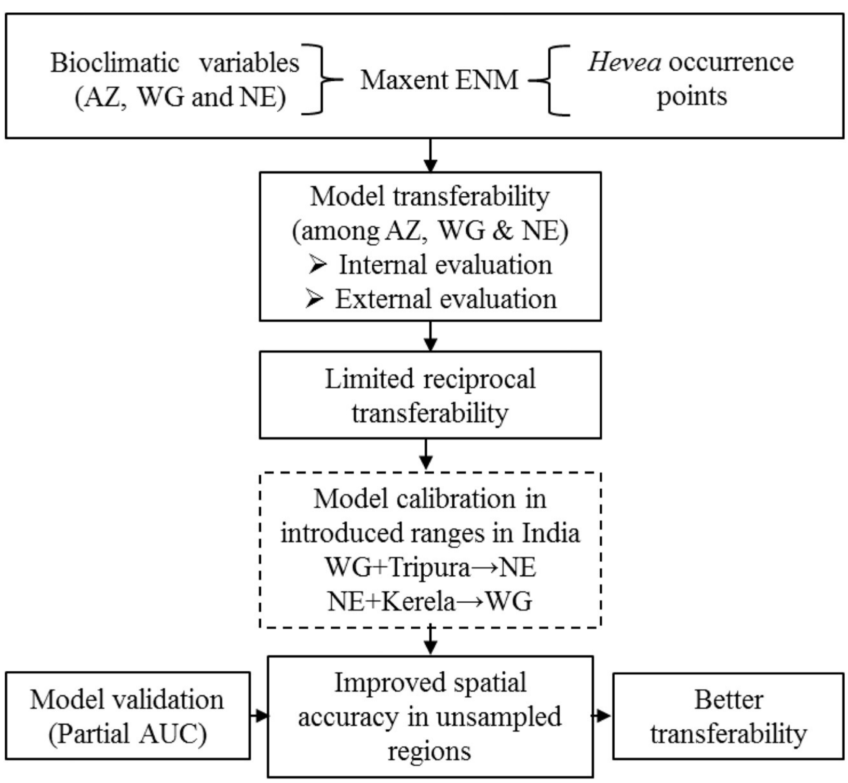

Fig. 2. Flow chart showing the overall methodology for improving transferability of Maxent model for *Hevea* species between NE and WG regions of India. Model transferability was tested among native (AZ) and introduced (WG, NE) ranges. *Hevea* distribution model was developed for all regions considering the respective occurrence data for model calibration (internal evaluation). Based on native range (AZ) of species distribution, the *Hevea* distribution was modelled in introduced ranges (WG, NE) (external evaluation). In order to improve the reciprocal transferability between the introduced range model calibration was done based on pooled occurrence points as indicated in dotted box.

based on number of sample points available for model training (Phillips and Dudik, 2008). Ten replications of the model were run, with 75% occurrence points as training site and 25% of the points as test sites. Regularization multiplier was followed as default value of '1'. The maximum iterations were fixed at 1000 with convergence threshold of 0.00001 and subsample replicated run type in order to allow the program to run up to the sufficient threshold levels. The background 10,000 points were selected randomly by the default settings of the model.

2.5. Climate comparison between introduced regions

To assess the heterogeneity of the climate space occupied by the *Hevea* in both introduced range, Welch's *t*-test and Levene's test were carried out (Mandle et al., 2010). The climate spaces occupied by introduced population of WG and NE region were extracted by superimposing species presence points on all bioclimatic variable grids of 30 arc sec resolution. Sampling through spatial analysis tools in Arc-GIS 10 was used to extract the climate values using the species presence point shape file. The nearest neighbour technique was used to resample the data points and the output data is generated in tabular form. The difference in the mean and breadth of climate envelope of introduced ranges were tested using Welch's *t*-test and Levene's test for homogeneity of variance in SPSS 17 (Mandle et al., 2010). Data extracted from these climate raster was compared using boxplot between two introduced populations for visual comparison. Boxplot is considered to give a good sense of data distribution with the help of median, minimum, maximum, and the first and third quartiles, which indicate the extent of data spread near median and extremes (Upton and Cook, 1996). The interquartile range (IQR) overlap between native and introduced region was used to classify the climate variables. The IQR is equal to the difference between third and first quartile, which is represented by the boxplot. The differences between the niche occupied in the two introduced range (WG and NE) were compared using niche overlap and niche identity test indices (Schoener's *D* statistic and Hellinger *I*) employing the ENMTools v.1.3 software. Overlap and identity metrics were generated from one pair of ASCII dataset of probability estimates of species' presence. Both metrics range from 0 (no similarity) to 1 (overlapping).

2.6. Reciprocal transferability between introduced ranges of Hevea

To test the reciprocal transferability between the niche models developed for *Hevea*, the model was initially calibrated with one introduced region (WG) and projected to the other introduced region of India (NE) (WG to NE) and vice-versa (NE to WG) which are geographically quite apart and climatically very dissimilar. A modified method was proposed to consider both introduced ranges for calibrating the model and then projecting to the other region to achieve better transferability with more spatial accuracy. The Maxent ENM was first calibrated with WG and Tripura and projected to NE for testing model transferability in one way. Further, the reverse transferability was assessed by calibrating the model with NE and Kerala and projected to WG region.

2.7. Partial AUC: a test for model accuracy

Performance of ENMs predicting the potential niche of a species is traditionally assessed by calculating the area under curve (AUC) of the receiver operator curve (ROC) (Fielding and Bell, 1997). Using this method, the commission error and omission error are given similar weightage. In Maxent model AUC is not an appropriate method of accuracy assessment because, it is a presence-only method (Lobo et al., 2008; Peterson et al., 2008). In this case, the average AUC value from the whole ROC space is not important. Instead, AUC values of the portion of ROC curve is more meaningful where omission and commission error is the minimum. For this reason, analysis of model performance using partial AUC procedure was carried out (Barve, 2008). In this procedure, ROC curve is a plot of sensitivity versus the proportion of the study area predicted as species' presence. The region of ROC space where the omission error is less than user defined variable (E) is considered for calculating partial AUC (here we used E = 10%, and thus allowed up to 10% omission in our partial ROC calculations) (Slater and Michael, 2012). The partial AUC (pAUC) was calculated using the partial ROC tool provided by the Biodiversity Institute, Lawrence, KS, Ver1.0 (Barve, 2008).

2.8. Transferability index estimation

Randin et al. (2006) has developed an index called transferability index (TI) (Eq. (1)) that numerically assesses the transferability of an ENM across two regions (Randin et al., 2006):

$$TI = \frac{\frac{1}{2}\left(\left(1-\frac{|AUC_{A\to A}-AUC_{A\to B}|}{0.5}\right)+\left(1-\frac{|AUC_{B\to B}-AUC_{B\to A}|}{0.5}\right)\right)}{1+\left|\left|\frac{AUC_{A\to A}-AUC_{A\to B}}{0.5}\right|-\left|\frac{AUC_{B\to B}-AUC_{B\to A}}{0.5}\right|\right|}, \quad (1)$$

$AUC_{regA \to regA}$ (internal evaluation) indicates the AUC values, when the model is calibrated in region A and projected in the same region. $AUC_{regA \to regB}$ (external evaluation) indicates the AUC values, when the model is calibrated in region A and projected in region B. The transferability index (TI) is based on the decrease of the AUC coefficient when switching from the internal ($AUC_{regA \to regA}$ and $AUC_{regB \to regB}$) to the external ($AUC_{regA \to regB}$ and $AUC_{regB \to regA}$) evaluation for both regions. The TI varies from 0 to 1 and is at its maximum when the difference between $AUC_{regA \to regB}$ and $AUC_{regB \to regA}$ is zero. This index is based on statistical accuracy of the model (AUC) and this does not include the reciprocal spatial prediction of distribution of the species (Randin et al., 2006). Maxent model was calibrated and projected for WG and NE region independently (internal evaluation). On the other hand, the model is calibrated for WG and projected on NE and calibrated for NE and projected to WG (external valuation). To compare the transferability index between native and introduced population of the species, model was calibrated with AZ region and projected to WG and NE region and vice-versa. Though, the relevance of partial AUC has been well established in recent years for the purpose of estimating the accuracy levels of the presence-only data based ENMs, transferability index based on AUCs is adapted in the present study. This is because of the objective of the study is to compare the spatial transferability between regions, not the comparison between ENMs (Elith et al., 2006; Terribile et al., 2010).

2.9. Estimation of niche similarity

Schoener's *D* and Hellinger's *I* statistics were used to measure the niche similarities of *Hevea* species between two introduced ranges in India and introduced range with native (Amazonian valley) range. These two indices were estimated by testing the similarities between the estimated probability of species presence using ENMTools (Warren and Seifert, 2010; Warren et al., 2008). The metrics of *D* and *I* were calculated by taking difference in the suitability score of each grid cell. These two indices range from 0 (niche are completely dissimilar) to 1 (niches are identical) (Warren et al., 2010). This is widely used in several studies to identify the niche overlapping among different species and regions (McCormack et al., 2010; Peterson, 2011).

3. Results

3.1. Internal and external evaluation of model transferability

Modelling of *Hevea* species distribution in its native range (AZ) using Maxent model has resulted a good matching with the provinces, Rondonia, Mato Grasso and Acre which are known as centre of origin of the species (Ong et al., 1983). Native niche based projection of species

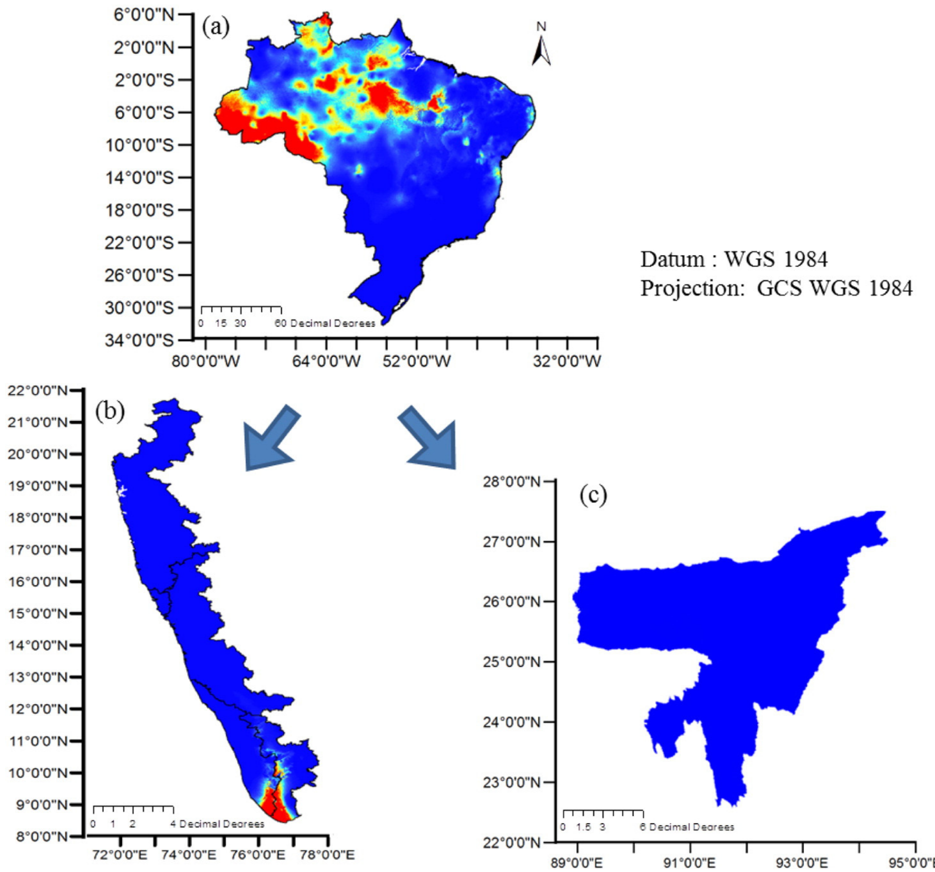

Fig. 3. Map showing the Maxent model predicted present distribution of *Hevea* species in its (a) native range (AZ) and projected distribution of the species in its introduced ranges, WG (b) and NE (c), based on the native niche.

distribution in one of its introduced ranges (WG) of India indicated that species distribution may be limited to Kannyakumari district of Tamil Nadu state and southern part of Kerala state (Fig. 3). However, the model could not project the suitable regions for *Hevea* species distribution in NE when the model was calibrated with occurrence points of AZ region. In introduced ranges, when model was calibrated for WG and projected to NE (external evaluation), south and western parts of Tripura, western parts of Assam and Meghalaya showed suitability values between 0.62 and 0.85. The northern parts of Assam along the state boundary of Meghalaya also showed suitability range of 0.31–0.38. The model predicted suitable regions are comparable with known distribution of species (Rubber statistics, Rubber Board, India) (Fig. 4). On the contrary, Southern parts of Mizoram were highlighted with the suitability values between 0.23 and 0.38, where there is no known occurrence record of *Hevea* plantation at present. The distribution of *Hevea* species in WG is simulated based on the presence data of the same region (internal evaluation). The results indicate that Southern parts of WG, which includes major portion of Kerala and parts of Tamil Nadu, have the maximum suitability

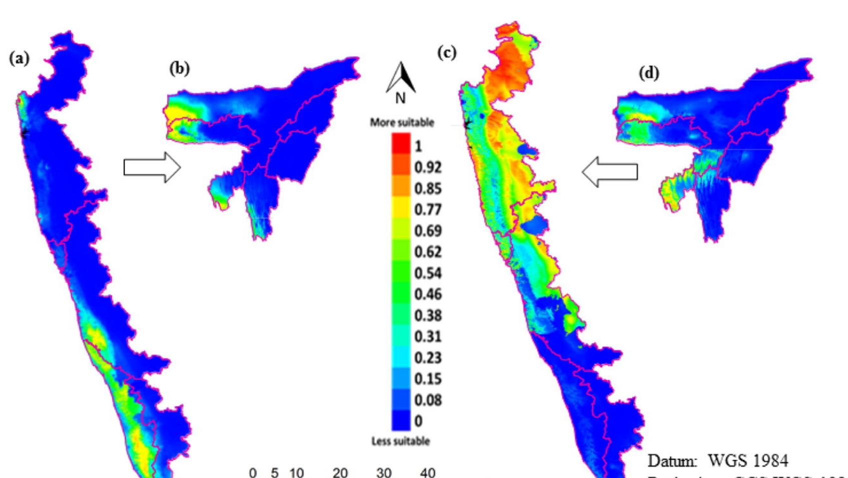

Fig. 4. Map showing the distribution of *Hevea* niche generated through model calibrated with WG (a) and projected to NE (b). Projection in NE shows better transferability. Projection of *Hevea* niche in WG (c) based on the calibration with NE (d). Projection in WG did not highlight Kerala, the most prominent *Hevea* growing state of India.

range of 0.77 to 0.92, surrounded by lower suitability range of 0.46 to 0.69 extending up to the mid-costal Karnataka with some pockets range between 0.77 and 0.85. In northern WG, there are areas with suitability range of 0.23 to 0.31 along with the border of Gujarat (Fig. 4).

The spatial accuracy is limited when the test for reciprocal transferability is carried out i.e., when the model is calibrated for NE and projected to WG. Northern WG, coastal Karnataka to Gujarat state boundary at the north shows suitability for growing *Hevea* species with a range of 0.62 to 1. Extreme north of WG shows the range of 0.92 to 1.0. However, southern parts of WG failed to exhibit suitability for growing *Hevea* species showing <0.08 values (Fig. 4). Therefore, it is found that model transferability from NE to WG could not predict the major *Hevea* species growing regions (Kerala) as suitable regions. However, internal evaluation in NE region has indicated that South and West Tripura, western parts of Assam are under the most suitable region with 0.69 to 0.85 values. Lower Assam, northern parts of Mizoram and western Meghalaya showed suitability values between 0.31 and 0.62 indicating the range of moderate suitability.

3.2. Assessment of transferability

Spatial transferability of the ENM for predicting the distribution pattern of *Hevea* was assessed through transferability index (TI) calculated based on internal evaluation and external evaluation (Randin et al., 2006). The TI was found to be 0.72 between the species' native range (AZ) and NE region, 0.83 between native and WG and 0.93 between WG and NE indicating better transferability of the model among these regions (Table 2). However, this is not always the indication of accurate spatial prediction. To improve the spatial accuracy of prediction in different geographical regions so that model prediction is more corroborative to real world, model complexity was reduced by minimising the number of input predictive variables. Asymmetrical prediction of spatial distribution of *Hevea* was observed as a function of model calibration site. In the present study, ENM transferability between the two introduced ranges of *Hevea* species indicate that spatially accurate transferability can be achieved only in 'WG to NE' direction, not in 'NE to WG' direction. This could be due to the difference in climate envelope occupied by the species in these two regions. The difference in climate envelope occupied by the species is due to difference in the time period taken for the process of introduction in respective regions (Strubbe et al., 2013). In other words, it is the history of introduction that also matters for accurate transferability. Similar impact of on-going colonization of *Hevea* in NE is seen in model projection, where the species is yet to be planted in many possible climatically suitable regions. Therefore, model calibrated in NE shows less accurate projection in WG. In the alternate approach, the model was trained using the pooled species presence in the introduced range of NE and Kerala and more spatially accurate transferability was achieved indicating the importance of both introduced ranges for model calibration.

3.3. Better transferability using pooled occurrence data

When the model is calibrated with pooled occurrence of WG and Tripura and projected to NE region, spatial niche distribution of *Hevea* species alters. In WG, southern region shows highest suitability with a range of 0.77–0.92 range of values. There are areas in southern parts of Tamil Nadu, entire Kerala and the region extending up to mid-coastal Karnataka with suitability values of 0.31 to 0.54. Eastern parts of the WG show least suitable regions with <0.08 probability values (Fig. 5a, b).

In NE region, large area in western and northern parts of Assam recorded suitability values within the range of 0.77 to 1. There are isolated patches in Tripura and lower Assam with similar range of suitability. Upper Assam is highlighted with large areas that are predicted as suitable for *Hevea* species with 0.38–0.62 range of suitability (Fig. 5c).

In reciprocal model projection, the model is calibrated with NE and Kerala and projected to WG. Model has predicted suitable regions for *Hevea* species with good accuracy in southern parts WG with highest suitability of 0.77–0.92. The areas with moderate suitability of 0.46 to 0.69 are extended towards northern WG. The isolated areas with lower suitability (0.31–0.38) are observed in parts of Karnataka and Maharashtra. The predicted distribution of *Hevea* niche is quite similar with the actual distribution of the species as per the records of Indian Rubber Board, the governmental agency responsible for promoting *Hevea* cultivation (Fig. 5d–f).

In NE region, South and West Tripura, western parts of Assam show highest suitability 0.77 to 0.92 probability values. The South western parts of Mizoram and western parts of Meghalaya are predicted as moderate suitable region with 0.38 to 0.54 values. Some areas in northern Assam along with the boundary Meghalaya show lower suitability (0.23–0.38). Rest of the NE is found to be least suited for *Hevea* with <0.08 suitability values (Fig. 5d).

3.4. Model accuracy

Performance of ENMs predicting the potential niche of a species is traditionally assessed by calculating the area under curve (AUC) of the receiver operator curve (ROC) (Fielding and Bell, 1997). The ROC describes the relationship between the proportion of correctly predicted and observed presences i.e., sensitivity and the proportion of incorrectly predicted observed absences i.e., (1-specificity) over the range of threshold values between 0 and 1. Model derived AUC is compared to the AUC of a random predictive model of AUC = 0.5 and model with an AUC above 0.75 are normally considered useful (Elith, 2006). Using this method, the commission error and omission error are given similar weightage. Recently, feasibility of applying this procedure for assessing the model accuracy in Maxent model was criticized due to non-availability of true absence data (Peterson et al., 2008; Lobo et al., 2008). Accuracy assessment through partial AUC (pAUC) procedure revealed that models calibrated for WG resulted better projection in NE region with pAUC values of 1.5 (±0.13) (Table 4). The model accuracy both in terms of spatial accuracy and pAUC values suffered when model transferability was tested in reverse direction (Fig. 6 and Table 3). However, model accuracy could be improved when it was calibrated with pooled occurrence points of NE and Kerala (two introduced ranges for *Hevea* in India) and projected to WG. The pAUC value was 1.25 (±0.11) with overall AUC of 0.881. But, calibration with pooled occurrence WG and Tripura has resulted in overall AUC of 0.927 and pAUC of 1.53 (±0.06) indicating better transferability in case of 'WG to NE' model (Table 3).

3.5. Comparison of climate space occupied by the species

Differences in the mean and breadth of two introduced climate spaces examined using Welch's *t*-test and Levene's test indicated that climate space occupied by *Hevea* was significantly different between two introduced ranges of the species, reflecting the wide range of climate in which the species can survive (Table 4). Introduced population showed different range of mean diurnal temperature (difference between monthly mean of maximum and minimum temperature) ($t = 201.2$, $df = 58.95$, $p < 0.001$). The range of diurnal temperature fluctuation in compared to that annual range (isothermality, Bio3) is significantly different in two introduced ranges of *Hevea* ($t = 1025$, $df = 58.26$, $p < 0.001$).

Table 2
Transferability index based on internal evaluation (calibrated and projected in same region) and external evaluation (calibrated and projected in different region). Values in parenthesis indicate the standard deviation among replicated model runs.

Calibration region	Projection region	Transferability index
Native range	Western Ghats region	0.83 (±0.014)
Native range	North-eastern region	0.72 (±0.02)
Western Ghats region	North-eastern region	0.93 (±0.03)

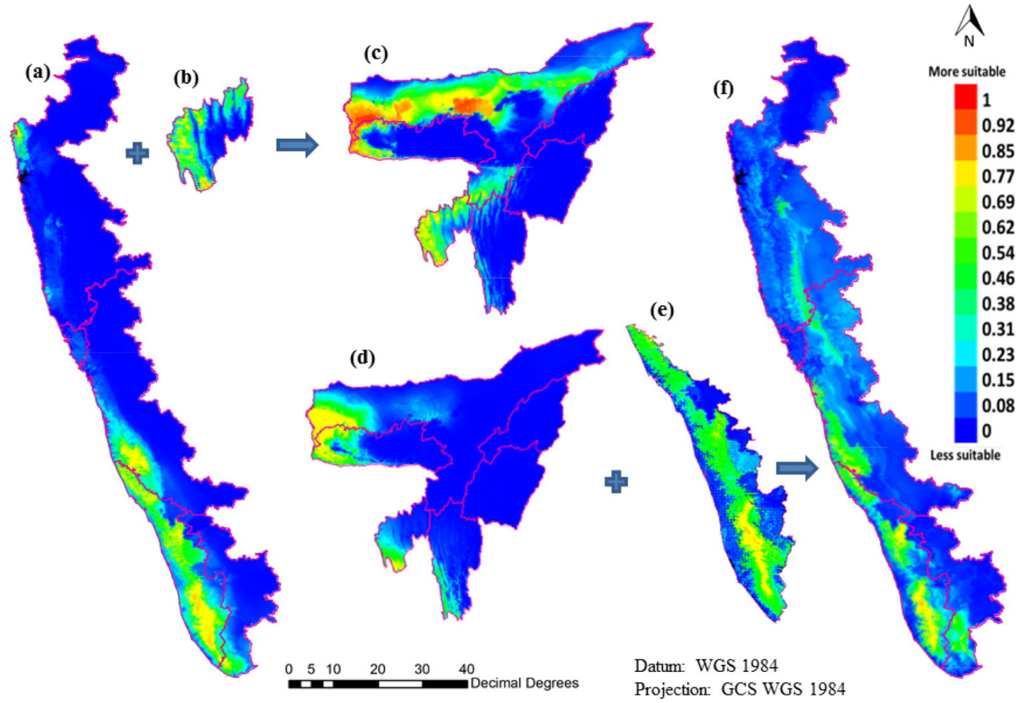

Fig. 5. Improved model transferability was achieved through calibrating the ENM with pooled presence points of WG (a), Tripura (b) and projected to NE (c) region. Calibrated with pooled presence points of NE (d) and Kerala (e) and projected to WG (f).

The temperature seasonality (Bio4) is found to be different in introduced regions of the species ($t = 2520$, $df = 89.76$, $p < 0.001$). *Hevea* occupies broader range of annual temperature (Bio7) in WG than in NE ($t = 876$, $df = 58.9$, $p < 0.001$). Precipitation in driest month (Bio14) shows broader range in WG than in NE ($t = 62$, $df = 55.35$, $p < 0.001$) and precipitation seasonality (Bio15) exhibits similar trend ($t = 73$, $df = 61.5$, $p < 0.001$). *Hevea* occupied regions of WG receives more precipitation of driest quarter (Bio17) ($t = 44$, $df = 55.34$, $p < 0.001$) and precipitation of coldest quarter (Bio19) ($t = 99$, $df = 53.92$, $p < 0.001$) compared to NE. Pearson correlation coefficients of 19 bioclimatic variables indicate that Bio5, Bio8 and Bio10 were highly correlated and therefore excluded from the boxplot analysis for further visual interpretation. Boxplot analysis of remaining 16 bio-climate variables of two introduced region (WG and NE) indicate that Bio2, Bio3, Bio4, Bio6, Bio14, Bio15, Bio17 and Bio19 are non-overlapping between two regions and therefore these variables were included for final model run (Fig. 7).

3.6. Niche similarity

Ecological niche similarity between introduced ranges is indicated by two indices called Schoener'*D* and Hellinger *I* derived by ENMTools software. Both indices range from 0 (no similarity) to 1 (identical). Schoener'*D* and Hellinger *I* recorded 0.521 ($\pm$0.003) and 0.677 ($\pm$0.007) respectively between WG and NE region, which shows the evidence of dissimilar niche occupied by the *Hevea* species in these two introduced ranges. Both WG and NE range were also compared with the native range of *Hevea* for niche similarity. *Hevea* niche in WG is highly divergent from its native range [$D = 0.297$ ($\pm$0.004), $I = 0.415$ ($\pm$0.007)]. Similarly, the niche similarity between NE and native

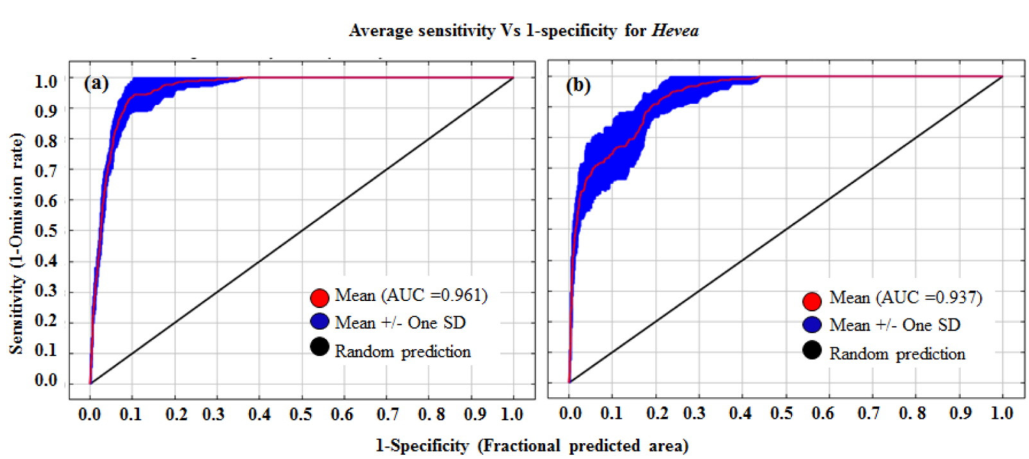

Fig. 6. Receiver operating characteristic (ROC) curve indicating the test AUC values averaged over the replicate runs for (a) Model calibrated in WG and projected to NE (b) calibrated with NE, projected to WG.

Table 3
Area under ROC curve (AUC) and partial AUC (pAUC) of models developed with different calibration and projection regions.

Calibration region	Projection region	AUC (±SD)	pAUC (±SD)
WG	NE	0.912 (±0.013)	1.50 (±0.133)
NE	WG	0.919 (±0.024)	1.097(±0.027)
WG and Tripura	NE	0.927 (±0.012)	1.53 (±0.066)
NE and Kerala	WG	0.881 (±0.020)	1.25 (±0.115)

range is not better than random (D = 0.498 (±0.004), I = 0.5 (±0.001)) (Fig. 8).

4. Discussion

4.1. Importance of introduced range for transferability of ENM

Application of ENMs in the studies on evolutionary relationship of species with the environment has provided insight into species niche dynamics (Beaumont et al., 2009; Warren et al., 2010). The potential niche of a species is difficult to be determined based on only its native range alone in certain species because of its intrinsic tolerance to climatic variations and ability to adapt to different climatic conditions. In the present study, modelling of present niche distribution of *Hevea* species in India based on its native range was not fully successful, strongly suggesting that the native niche of this species does not fully define its present climate envelope. Therefore, it is important to consider existing knowledge about the spectrum of introduced ranges of the species to determine the potential niche in other regions outside the existing niche (Loo et al., 2007). Though, better statistical transferability was gained by removing mutually correlated variables, the spatial accuracy could not be fully achieved (Verbruggen et al., 2013). Improvement of niche based model accuracy depending on inclusion of more introduced range as training sites indicate the importance of new regions for spatially accurate model development.

4.2. Uncertainty in climatic niche conservatism between introduced ranges

Niche based modelling approach offers new opportunity to study the introducing potential of species. However, the climatic niche of a species is assumed to be conserved across time and space (Pearman et al., 2007), an element of uncertainty in niche conservatism that has been shown in some studies. Usual practices of training model in the native range and projecting in unsampled region fail to predict invasive potential of certain species (Fernández and Hamilton, 2015; Randin et al., 2006). Similar findings in *Hevea* niche distribution is observed in the present study that showed asymmetrical model transferability among native (AZ), WG and NE, introduced ranges in India. It is worth mentioning in this context that WG range is considered as early introduced regions for *Hevea* and NE region is the recently introduced region in India (Sinha, 2010). Asymmetric niche model transferability between two introduced ranges of India indicates that model is sensitive to the distributional range of the species, which is used as calibration sites for the ENM. One of the causes for this asymmetric model transferability could be due to wide range of factors contributing to the distribution of *Hevea* trees in introduced regions including anthropogenic factors other than climate and soil (Ray et al., 2016). In another study, this has been shown that *Hevea* are unexpectedly not affected by low soil moisture conditions of dry sub-humid regions of Thailand (Clermont-Dauphin et al., 2013).

Table 4
Testing of differences in the mean and breadth of native and introduced ranges of *Hevea* using robust test of equality of means (Welch statistic) and test of homogeneity of variances (Levene statistic).

	Robust test of equality of means			Test of homogeneity of variances		
Variables	Welch statistic	df1	df2	Levene statistic	df1	df2
Bio1	63.958	2	89.786	9.387	2	245
Bio2	201.258	2	58.958	13.266	2	245
Bio3	1025.407	2	58.262	27.101	2	245
Bio4	2520.013	2	89.766	3.456	2	245
Bio5	17.744	2	68.343	5.430	2	245
Bio6	799.513	2	60.554	26.814	2	245
Bio7	876.281	2	58.901	19.096	2	245
Bio8	84.835	2	107.547	8.795	2	245
Bio9	720.200	2	69.703	12.224	2	245
Bio10	29.394	2	95.832	7.390	2	245
Bio11	654.762	2	80.535	15.293	2	245
Bio12	24.166	2	102.334	27.582	2	245
Bio13	169.239	2	162.319	56.389	2	245
Bio14	62.190	2	55.357	62.542	2	245
Bio15	73.769	2	61.508	103.851	2	245
Bio16	141.179	2	160.903	38.886	2	245
Bio17	44.689	2	55.345	64.721	2	245
Bio18	305.484	2	59.804	25.125	2	245
Bio19	99.372	2	53.929	196.637	2	245

4.3. Implications of the present study

One of the most important practical implications of ENMs is to predict the new geographical areas where a cultivated species can get introduced (Evans et al., 2010; Trisurat et al., 2009). This is generally achieved by establishing a relationship between species presence and climate variables prevailing in the same locations and then predicting new areas based on this empirical relationship. In new introduced range, the species may be favoured by other biotic and abiotic variables that allow the species to grow in diverse conditions. An excellent review on niche, biogeography and species interaction supports the understanding on similar interaction among various input variables, bio-geographical patterns of *Hevea* plantations and its niche characteristics (Pearman et al., 2007). Biotic and abiotic variables associated with certain biogeography would have been excluded from either of the introduced range of the species, and therefore, the model trained in either of introduced range will fail to account for new climate that the species might have occupied recently. For this reason, pooled approach of including both introduced ranges for model calibration, WG and NE has resulted better prediction of introducing potential of the species as this can represent aptly the climatic envelope the species occupies in introduced ranges. On the other hand, there could be possibilities of evolving fundamental niche in the introduced range after the introduction of the species (Broennimann et al., 2007; Dietz and Edwards, 2006; Gallagher et al., 2010; Pearman et al., 2007; Warren et al., 2010). However, other studies have shown that climatic niche shifts are rare among terrestrial plant invaders between native and introduced ranges (Petitpierre et al., 2012). When a species is introducing into new regions, it becomes challenging to evaluate whether there are changes in realized niche or fundamental niche of the species.

5. Conclusions

The ENM was employed to predict the potential of *Hevea* species to get introduced in two distinct bio-geographical regions of India. The model predicted the potential regions in WG and NE for future introduction of the *Hevea* species through calibrating and projecting in same region. Calibration in early introduced region (WG) of *Hevea* species and projection to lately introduced region (NE) has resulted in reasonably accurate spatial transferability of the model. However, the reciprocal transferability of the model was limited. This indicates that the contributing climate variables for introducing the species in two regions are different. This may be due to the difference in environmental tolerance levels of the species in two regions. In addition to that, involvement of anthropogenic pressure on the expansion of *Hevea* plantation

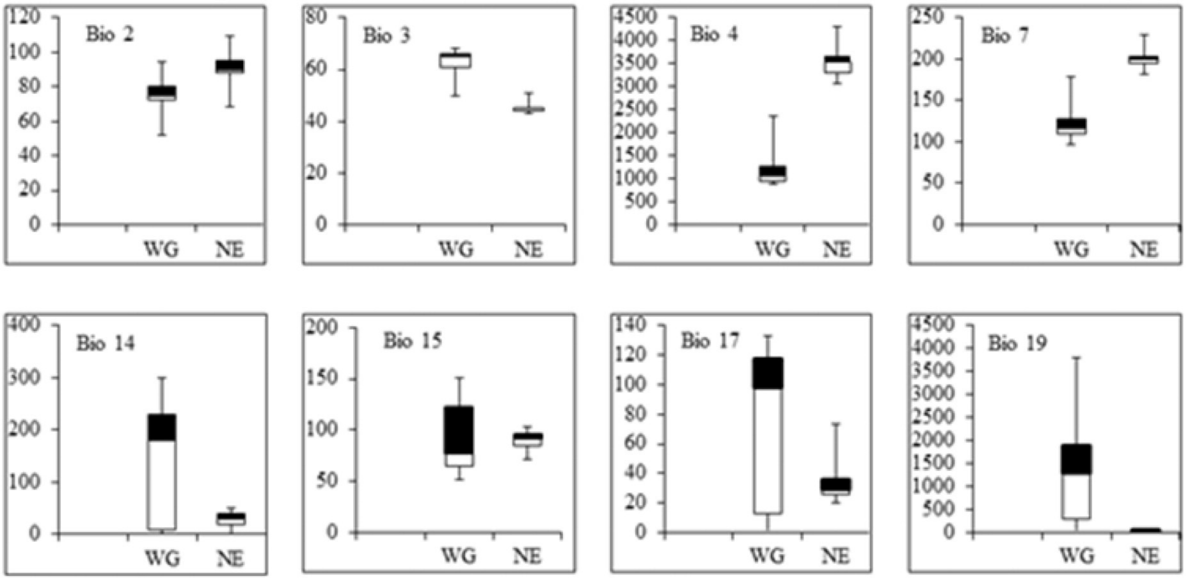

Fig. 7. Direct comparison of climate variables. *Hevea* species presence associated 8 climate variables were compared by boxplot analysis for two introduced distributional region (WG and NE). Annual mean diurnal range (×10) (Bio2, °C), isothermality (Bio3, %), temperature seasonality (Bio4, °C), annual temperature range (Bio7, °C), precipitation of driest month (Bio14, mm), precipitation seasonality (Bio15, %), precipitation of driest quarter (Bio17, mm) and precipitation of coldest quarter (Bio19, mm) are expressed in Y axis in each box plot.

has made the species to tolerate wide range of climatic variables. In the present study, *Hevea* species samples failed to represent the actual climate envelop indicating the existence of unfilled niche for *Hevea* in NE. Model transferability was improved by an alternate approach of pooled occurrence points from both introduced ranges used for model calibration. The already introduced range (Kerala and Tripura) represent the actual climate envelop occupied by the species. Therefore, there may be involvement of other (non-climate) variables such as land use and land cover changes, socio-economic conditions of the regions and governmental support systems etc. contributing to the niche distribution of *Hevea* species in both introduced ranges of *Hevea* species in India.

Conflict of interest

The authors declare that there is no conflict of interest in publishing their work.

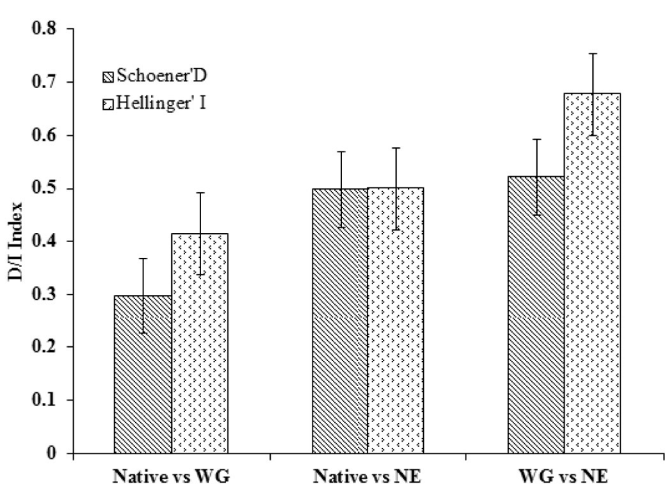

Fig. 8. Niche similarity *Hevea* among native range, WG and NE regions indicated by Schoener'*D* and Hellinger'*I* derived using ENMTools.

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References

Albert, C.H., Yoccoz, N.G., Edwards Jr., T.C., Graham, C.H., Zimmermann, N.E., Thuiller, W., 2010. Sampling in ecology and evolution bridging the gap between theory and practice. Ecography 33, 10281037. http://dx.doi.org/10.1111/j.1600-0587.2010.06421.x.

Anuja, A.R., Kar, A., Mathur, V.C., Jha, G.K., 2012. Input delivery processing and marketing of natural rubber: the role of producers cooperatives in Kerala. Agric. Econ. Res. Rev. 25, 379–386.

Araujo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. J. Biogeogr. 33, 1677–1688.

Barve, N., 2008. Tool for Partial-ROC. Version 1. Biodiversity Institute, Lawrence, KS (Available: http://kuscholarworks.ku.edu/dspace/handle/1808/10059).

Beaumont, L.J., Gallagher, R.V., Thuiller, W., Downey, P.O., Leishman, M.R., et al., 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. Divers. Distrib. 15, 409–420.

Blossey, B., Notzold, R., 1995. Evolution of increased competitive ability in invasive nonindigenous plants — a hypothesis. J. Ecol. 83, 887–889.

Broennimann, O., Guisan, A., 2008. Predicting current and future biological invasions: both native and introduced ranges matter. Biol. Lett. 4 (5), 585–589.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T., Guisan, A., 2007. Evidence of climatic niche shift during biological invasion. Ecol. Lett. 10 (8), 701–709.

Chapman, A.D., 2005. Principles and methods of data cleaning — primary species and species-occurrence data, version 1.0. Report for the Global Biodiversity Information Facility, Copenhagen.

Clermont-Dauphin, C., Suvannang, N., Hammecker, C., Cheylan, V., Pongwichian, P., Do, F.C., 2013. Unexpected absence of control of rubber tree growth by soil water shortage in dry sub-humid climate. Agron. Sustain. Dev. 33 (3), 531–538.

Dean, W., 1987. Brazil and the Struggle for Rubber — A Study in Environmental History. Cambridge University Press.

Dietz, H., Edwards, P.J., 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology 87 (6), 1359–1367.

Dormann, C.F., Purschke, O., Marquez, J.R.G., Lautenbach, S., Schröder, B., 2008. Components of uncertainty in species distribution analysis: a case study of the great grey shrike. Ecology 89 (12), 3371–3386.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. http://dx.doi.org/10.1146/annurev.ecolsys.110308.120159.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, G., Nakamura, M., Nakazawa, Y., McC Overton, J., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29 (2), 129–151.

Evans, J.M., Fletcher, R.J., Alavalapati, J., 2010. Using species distribution models to identify suitable areas for biofuel feedstock production. GCB Bioenergy 2, 63–78. http://dx.doi.org/10.1111/j.1757-1707.2010.01040.x.

Fernández, M., Hamilton, H., 2015. Ecological niche transferability using invasive species as a case study. PLoS One 10 (3), e0119891.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the measurement of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.

Fourcade, Y., Engler, J.O., Rödder, D., Secondi, J., 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS One 9 (5), e97122. http://dx.doi.org/10.1371/journal.pone.0097122.

Gallagher, R.V., Beaumont, L.J., Hughes, L., Leishman, M.R., 2010. Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. J. Ecol. 98 (4), 790–799.

Garcia, K., Lasco, R., Ines, A., Lyon, B., Pulhin, F., 2013. Predicting geographic distribution and habitat suitability due to climate change of selected threatened forest tree species in the Philippines. Appl. Geogr. 22, 12–22.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.

Heikkinen, R.K., Marmion, M., Luoto, M., 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? Ecography 35, 276–288.

Hong, L.T., 1999. Rubberwood — processing and utilisation. In: Hong, L.T., Sim, H.C. (Eds.), Malayan Forest Records. Forest Research Institute Malaysia, Kuala Lumpur, pp. 1–15 (ISBN 983-9592-27-0).

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22, 415–427.

INCCA, 2010. Climate change and India: a 4 × 4 assessment. Indian Network for Climate Change Assessment. Ministry of environment and Forest, Government of India (www.moef.nic.in/downloads/public-information/fin-rpt-incca.pdf. Accessed on 21st May, 2014).

Jacob, J., 2000. Rubber tree, man and environment. In: George, P.L., Jacob, C.K. (Eds.), Natural Rubber: Agromanagement and Crop Processing. Rubber Reasearch Institute of India, Kottayam, pp. 509–610.

Jacob, J., Raj, U., 2012. Geospatial Technology for Acreage Estimation of Natural Rubber and Identification of Potential Areas for its Cultivation in Tripura State. National Remote Sensing Centre ISRO and Rubber Research Institute of India Rubber Board, Min. of Commerce & Industry, Govt. of India (Report number: NRSC-RC(S)-JULY-2012-TR-419, Affiliation: RRSS-South, NRSC).

Jiang, J., Wang, R., 2003. Hydrological eco-service of rubber plantations in Hainan Island and its effect on economic development. J. Environ. Sci. 15 (5), 701–709.

Krishnakumar, A.K., Meenattoor, R.J., 2003. Restoration of Denuded Lands in the North Eastern India Through Rubber Plantations. pp. 23–24 (Leisa India, December).

Lazo, D.J., Van Gils, H.A.M.J., Groen, T.A., Navarro-Cerrillo, R.M., 2016. Transferability of species distribution models: the case of *Phytophthora cinnamomi* in Southwest Spain and Southwest Australia. Ecol. Model. 320, 62–70.

Lobo, J.M., Jimenez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145–151.

Loo, S.E., Nally, R.M., Lake, P.S., 2007. Forecasting New Zealand mud snail invasion range: model comparisons using native and introduced ranges. Ecol. Appl. 17 (1), 181–189.

Mandle, L., Warren, D.L., Hoffmann, M.H., Peterson, A.T., Schmitt, J., et al., 2010. Conclusions about niche expansion in introduced *Impatiens walleriana* populations depend on method of analysis. PLoS One 5 (12), e15297. http://dx.doi.org/10.1371/journal.pone.0015297.

Mau-Crimmins, T.M., Schussman, H.R., Geiger, E.L., 2006. Can the invaded range of a species be predicted sufficiently using only native-range data? Lehmann love grass (*Eragrostis lehmanniana*) in the south western United States. Ecol. Model. 193, 736–746.

McCormack, J.E., Zellmer, A.J., Knowles, L.L., 2010. Does niche divergence accompany allopatric divergence in Aphelocoma jays as predicted under ecological speciation? Insights from tests with niche models. Evolution 64 (5), 1231–1244.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global biodiversity conservation: the critical role of hotspots. In: Zachos, F.E., Habel, J.C. (Eds.), Biodiversity Hotspots. Springer Publishers, London, pp. 3–22.

Mott, C.L., 2010. Environmental constraints to the geographic expansion of plant and animal species. Nat. Educ. Knowl. 3 (10), 72–81.

Ong, S.H., Ghani, M.N.A., Tan, A.M., Tan, H., 1983. New *Hevea* germplasm: Its introduction and potential. Proceedings of the Planters Conference Vol. 3. Rubber Research Institute of Malaysia, Kuala Lumpur, pp. 3–17.

Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F., 2007. Niche Dynamics in Space and Time. Vol. 23(3). Cell Press, pp. 149–157.

Peterson, A.T., 2011. Ecological niche conservatism: a time-structured review of evidence. J. Biogeogr. 38 (5), 817–827.

Peterson, A.T., Papes, M., Soberon, J., 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modelling. Ecol. Model. 213, 63–72.

Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C., Guisan, A., 2012. Climatic niche shifts are rare among terrestrial plant invaders. Science 335 (6074), 1344–1348.

Phillips, S.J., Dudik, M., 2008. Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31 (2), 161–175.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modelling of species geographic distributions. Ecol. Model. 190 (3), 231–259.

Pulliam, H.R., 2000. On the relationship between niche and distribution. Ecol. Lett. 3, 349–361.

Randin, C.F., Dirnbock, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? J. Biogeogr. 33, 1689–1703.

Ray, D., Behera, M.D., Jacob, J., 2014. Indian Brahmaputra Valley offers significant potential for cultivation of rubber trees under changed climate. Curr. Sci. 107 (3), 461–469.

Ray, D., Behera, M.D., Jacob, J., 2016. Predicting rubber tree distribution through ecological niche modelling with climate, soil and socioeconomic drivers. Ecol. Res. 31 (1), 75–91.

Rodgers, W.A., Panwar, H.S., 1988. Planning a Wildlife Protected Area Network in India. Project FO: IND/82/003 2 vols. FAO, Dehra Dun (339: 267 pp.).

Sehgal, J.L., Mandal, D.K., Mandal, C., Vadivelu, S., 1992. Agro-ecological Regions of India. In: Technical Bulletin No. 24. National Bureau of Soil Survey & Land Use Planning, ICAR, India, pp. 88–90.

Seoane, J., Carrascal, L.M., Alonso, C.L., Palomino, D., 2005. Species-specific traits associated to prediction errors in bird habitat suitability modelling. Ecol. Model. 185, 299–308.

Silvertown, J., 2004. Plant coexistence and the niche. Trends Ecol. Evol. 19, 605–611.

Sinha, A.K., 2010. Rubber plantation in Northeast India, hopes vs. concerns, the Tripura foundation. Published online: http://thetripurafoundation.org/art-rubber-prospect-tripura-and-north-east.

Slater, H., Michael, E., 2012. Predicting the current and future potential distributions of lymphatic filariasis in Africa using maximum entropy ecological niche modelling. PLoS ONE 7 (2), e32202. http://dx.doi.org/10.1371/journal.pone.0032202.

Soberón, J., Nakamura, M., 2009. Niches and distributional areas: concepts, methods, and assumptions. Proc. Natl. Acad. Sci. U. S. A. 106, 19644–19650. http://dx.doi.org/10.1073/pnas.0901637106.

Soberón, J., Peterson, A.T., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers. Inform. 2, 1–10.

Strubbe, D., Broennimann, O., Chiron, F., Matthysen, E., 2013. Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. Glob. Ecol. Biogeogr. 22 (8), 962–970.

Terribile, L.C., Diniz-Filho, J.A.F., Marco Jr., P, D., 2010. How many studies are necessary to compare niche-based models for geographic distributions? Inductive reasoning may fail at the end. Braz. J. Biol. 70 (2), 263–269.

Trisurat, Y., Alkemade, R., Arets, E., 2009. Projecting forest tree distributions and adaptation to climate change in northern Thailand. J. Ecol. Nat. Environ. 1 (3), 55–63.

Upton, G.J., Cook, I.T., 1996. Understanding Statistics. Oxford University Press.

Veloz, S.D., 2009. Spatial auto-correlated sampling falsely inflates measures of accuracy for presence-only niche models. J. Biogeogr. 36 (12), 2290–2299.

Verbruggen, H., Tyberghein, L., Belton, G.S., Mineur, F., Jueterbock, A., Hoarau, G., Gurgel, C.F.D., DeClerck, O., 2013. Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. PLoS One 8 (6), e68337.

Verheye, W., 1980. Growth and production of rubber. Soils Plant Growth and Crop Production Vol. II (124-168 pp.).

Warren, D.L., Seifert, S.N., 2010. Environmental niche modelling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol. Appl. 21 (2), 335–342.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62 (11), 2868–2883.

Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33 (3), 607–611.

Whittingham, M.J., Wilson, J.D., Donald, P.F., 2003. Do habitat association models have any generality? Predicting skylark *Alauda arvensis* abundance in different regions of southern England. Ecography 26, 521–531.

Wycherley, P.R., Mathew, N.M., 1992. The genus *Hevea* — botanical aspects. In: Sethuraj, M.R. (Ed.), Natural Rubber: Biology, Cultivation, Technology. Developments in Crop Science 23. Elsewier, Netherlands, pp. 50–66 (ISBN 0-444-88329-0).

Zhu, G., Bu, W., Gao, Y., Liu, G., 2012. Potential geographic distribution of brown marmorated stink bug invasion (*Halyomorpha halys*). PLoS One 7 (2), e31246. http://dx.doi.org/10.1371/journal.pone.0031246.