Species distribution models: ecological explanation and prediction of an endemic and endangered plant species (*Pterocarpus santalinus* L.f.)

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***Pterocarpus santalinus* L.f. (Red Sanders) is an endemic and endangered species largely confined to the southern portion of the Eastern Ghats, Andhra Pradesh, India. To understand its ecological and geographic distribution, we used ecological niche modelling (ENM) based on field sample-based distributional information, in relation to climatic and topographic datasets. Before modelling, hierarchical partitioning was used to optimize the choice of variables for better prediction and reliability. We used three ENM approaches, namely GARP, Maxent and BIOCLIM for predicting potential areas of occurrence. The ENM successfully reconstructed key features of the species geographic distribution, mainly in the forest tracts of Chittoor and Kadapa districts. GARP appeared to be more robust in prediction capabilities compared to BIOCLIM. The potential distributional area identified by these models falls mainly in regions not protected and experiencing high anthropogenic pressure owing to economic and medicinal use. The success of this model indicates that ENM-based approaches provide a promising tool for exploring various scenarios useful in the study of ecology, biogeography and conservation.**

Keywords: Ecological niche modelling, hierarchical partitioning, *Pterocarpus santalinus*, species distribution.

Introduction

MODELLING species ecological niche and its potential distributions is becoming a powerful tool for biogeographers, conservation biologists and ecologists in recent years[1–3]. Ecological niche modelling (ENM), also known as bioclimatic modelling or climate envelope modelling, has been applied increasingly to this task. This approach uses geo-referenced primary occurrence data for species, in combination with digital maps representing environmental parameters to build models characterizing ecological requirements of species. Then, such conditions are located on landscapes and maps created to indicate the distributional potential of the species[4–6]. With this approach, distributional shifts caused by changes in climate variables can be estimated based on the fact that the niche model is characterized in ecological space – conditions with which a species is associated at present can be sought on modelled future or past climate scenarios[7–9].

Rare and endangered species are increasingly being accorded high priority by world conservation agencies[10] to envisage long-term goals for conservation programmes, such as identifying critical biological community or areas particularly in need of protection[11]. Most species in danger of getting extinct are either ecologically unique or highly habitat-restricted, now totalling to 1,558,912 (ref. 12). Thus, identifying potential distribution of endemic and endangered species becomes essential in tropical region of the Eastern Ghats, where vast areas remain unexplored. Here, we explored three analytical approaches using ENM: OpenModeller GARP, Maxent and BIOCLIM that are based on presence-only data. We applied these methods to predict the potential distribution of *Pterocarpus santalinus* for biodiversity conservation and monitoring. We ran niche models and tested whether these have significant predictive power when applied to other sectors of the species overall distribution and used the methods to explore various aspects of the species, i.e. ecological and geographic distribution.

Methods

Study area

The Eastern Ghats are a discontinuous range of mountains along the eastern coast of peninsular India extending

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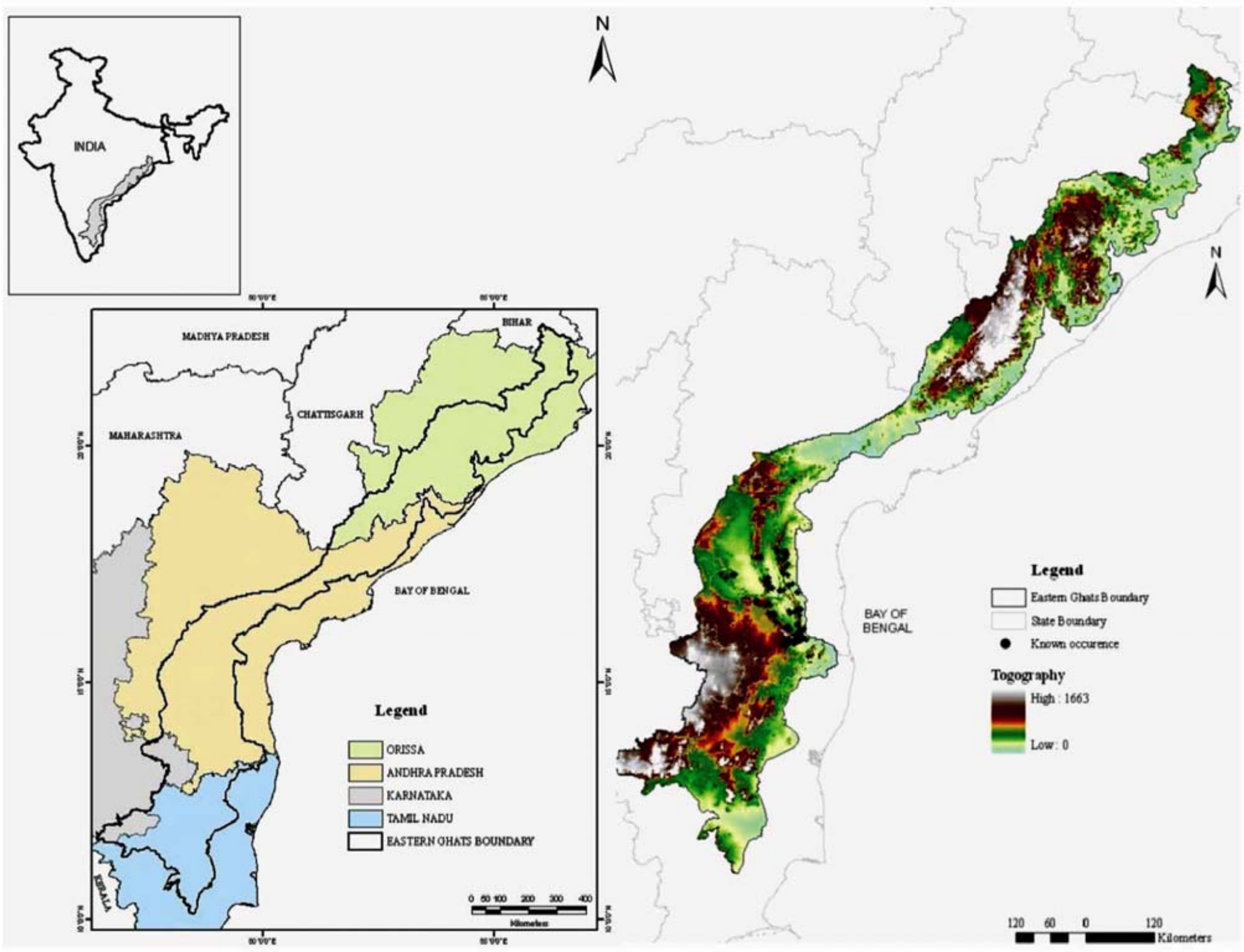

Figure 1. ***a***, Study area showing states of the Eastern Ghats and delineation of boundary analysed for modelling *Pterocarpus* distribution. ***b***, Spatial distribution of *Pterocarpus santalinus* occurrence overlaid on Digital Elevation Model (DEM) for the entire Eastern Ghats.

> 1750 km, with the average width of ~100 km (Figure 1). The Eastern Ghats are ancient 'tors' geologically older than the Himalayas and the Western Ghats. Majority of the Eastern Ghats lies in the state of Andhra Pradesh, which currently holds forested area of 44,637 sq. km, about 16% of the total geographic area of the state[13]. The forests in the state are broadly classified into tropical dry deciduous, tropical moist deciduous and tropical semi-evergreen types. The Eastern Ghats also harbour a wide range of wild crops (millet, rice) and other economic and medicinal plants. The endemic plants of this region are generally palaeo-endemics and can be extremely localized. They have very narrow distributional ranges and several studies indicate that they are in a gradual process of extinction[14,15].

Species ecological characteristics

Pterocarpus, commonly known as 'Raktachandan or Red Sanders' is a pan-tropical genus accommodating about 30 deciduous woody plant species. Only four species occur in India, viz. *P. dalbergioides* (Padauk) in the Andamans; *P. indicus* native to Malaysia that has been introduced and planted as an avenue tree in the Andamans, West Bengal, Tamil Nadu and Maharashtra[16] and *P. marsupium* (Indian Kino tree) in deciduous forests throughout mainland India. *P. santalinus* is an endemic and endangered species[17] distributed mainly in the southern Eastern Ghats (Figure 2)[17,18]. It forms a distinct dry Red Sanders-bearing forest. In Andhra Pradesh, it is restricted to Rayalaseema (Seshachalam Hills of Kadapa and Chittoor, Nigidi Hills of Anantapur, Nallamalais of Kurnool, and Veligonda Hills of Prakasham and Nellore)[19]. In Tamil Nadu, it occurs rarely up to 500 m elevation in the districts of Thiruvallur, Salem, Dharmapuri[20]. All four species are valued for their wood and all three except, *P. marsupium* are valued for a red pigment, *santalin*, which they produce. However, *P. santalinus* is particularly valued for its heavy, dark, claret-red heartwood, which yields 16% santalin. *P. santalinus* occurs in the hilly regions with hot and dry climates. It is a strong light demander and does not tolerate overhead shade or water-logged conditions.

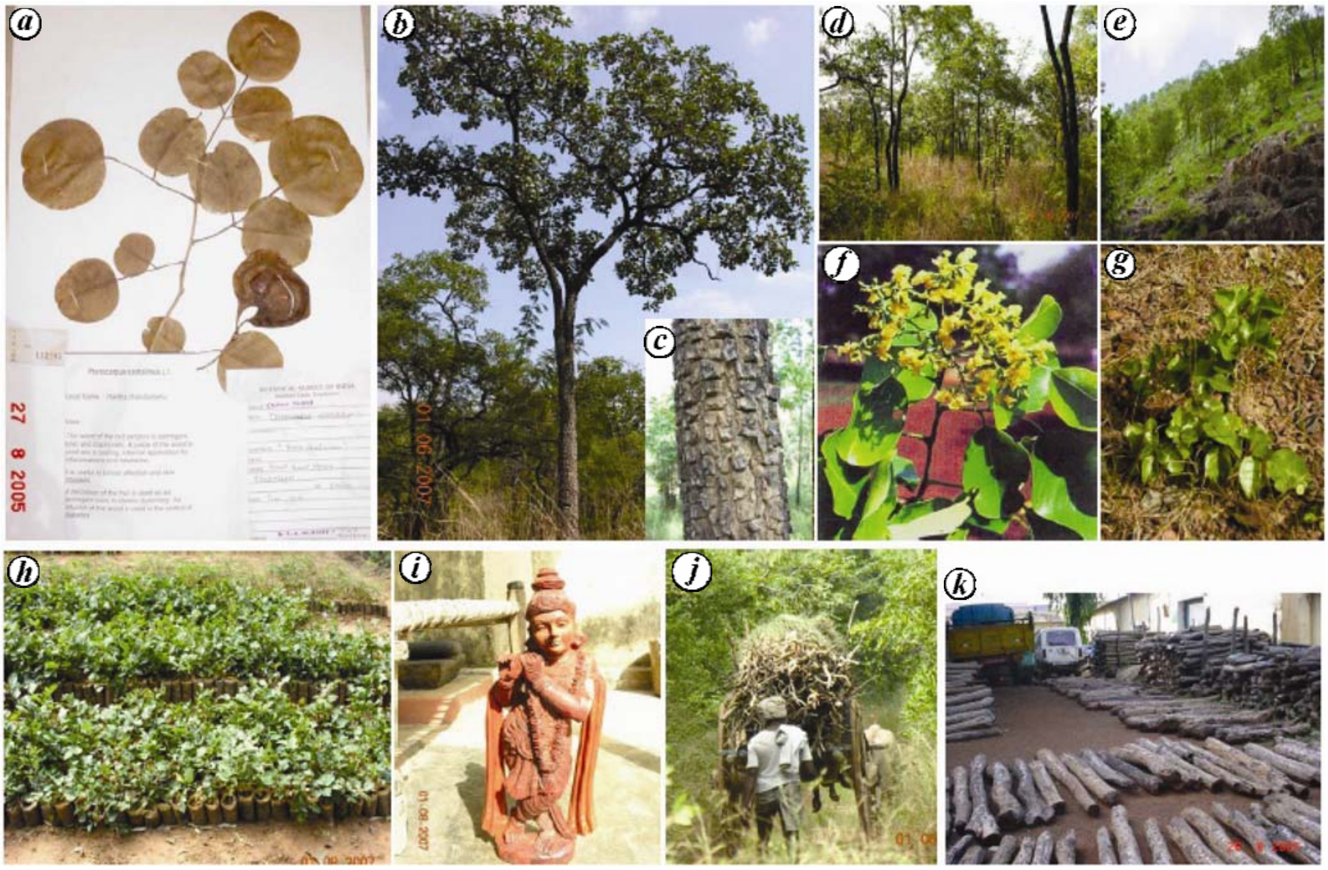

Figure 2. Field photographs, herbarium specimen, illegal felling and saplings of *Pterocarpus santalinus* observed during our field visit in Kadapa and Chittoor districts of Andhra Pradesh.

Input data

We collected 128 point locations for *P. santalinus* species from on-ground surveys using GPS during a regional biodiversity inventory at landscape level for the Eastern Ghats[21,22] (Figure 1). To include historical occurrences, herbarium specimen data were gathered from the Botanical Survey of India, Kolkata[23] and several regional flora literature surveys[24–27]. All records were geocoded via reference to large-scale (1 : 50,000) topographic maps. We also collected field data from line-transects laid at 21 different sites of the *Pterocarpus* occurrence in Kadapa and Chittoor districts. Individuals of ≥ 10 cm were enumerated along with herbs, shrubs and saplings in the line transect of 100 m × 10 m. Data were collected on height, girth at breast height, nature of anthropogenic disturbance, if any, and topographic characteristics like slope aspect and altitude. These data were further subjected to correspondence analysis for identifying communities of *Pterocarpus*.

Environmental datasets

We used 19 bioclimatic variables derived from globally interpolated datasets of monthly temperature and precipitation (described in detail in Hijmans[28]), including annual and seasonal aspects of temperature and precipitation that are presumed to be maximally relevant to plant survival and reproduction[29]. We also included elevation, slope, aspect and compound topographic index from the USGS HYDRO1k dataset[30]. Analyses were conducted at the native 30″ (~1 × 1 km pixels) spatial resolution of the environmental datasets.

Hierarchical partitioning

Identifying fewer response variables for a species presence/absence is always an implication for ENM. Hierarchical partitioning (HP) may offer a solution to this dilemma[31], as it considers all possible multivariate models in a multiple regression setting jointly to identify the most likely causal factors. This averaging is likely to alleviate multi-collinearity problems that are effectively ignored by single-model-seeking techniques. HP allows identification of predictor variables and their independent (*I*) and joint (*J*) influences on the response variable. In many ecological and conservation problems, one wishes to identify those predictor variables that have the greatest independent impact on species occurrences.

Model development

We used the Genetic Algorithm for Rule Set Prediction (GARP) under the Open Modeller (OM) implementation[32]. OM aims to provide a flexible, user-friendly, cross-platform environment in which the entire process of niche modelling can be carried out. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection. First, a method was chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules) and then applied to the training data and a rule was developed. Rules may evolve by a number of means (e.g. truncation, point changes, crossing-over among rules) to maximize prediction. Further, predictive accuracy was evaluated based on 1250 points resampled with replacement from the intrinsic testing data and 1250 points sampled randomly from the study region as a whole to represent pseudo absences. The change in predictive accuracy from one iteration to the next was used to evaluate whether a particular rule should be incorporated into the model and the algorithm runs either 1000 iterations or until convergence. We developed 100 replicate model runs for *Pterocarpus* and filtered out suboptimal models based on characteristics in terms of omission (leaving areas of known presence out of the predictions) and commission (including areas not actually inhabited) error statistics. Following recent recommendations[33] and also to represent a balance between optimizing model selection and practicalities of computing time required for the analysis, we selected the best models in DesktopGARP using a 0% extrinsic hard omission threshold and 50% commission threshold. Experiments with different thresholds indicate that results are quite robust to minor variation in the thresholds chosen. Throughout we masked analyses to include only the Eastern Ghats region.

Maxent models were developed using a software[34] that has been described and tested in detail in recent publications[35,36]. Maxent focuses on fitting a probability distribution for occurrence of the species in question to the set of pixels across the study region, based on the idea that the best explanation to unknown phenomena will maximize the entropy of the probability distribution, subject to the appropriate constraints. In the case of modelling ecological niche of species, these constraints consist of the values of those pixels at which the species has been detected[37]. In general, we used default parameters for Maxent models, which produce cumulative probabilities of occurrences. We imported the output file into ArcView as integer grids for further analysis. BIOCLIM (bioclimatic analysis and prediction system) can be used to identify the areas or niches to which the organisms can invade based on the climatic and ecological features of the sampled data points of the known occurrence of the species. An iterative procedure was used. In all iterations, the ‘value’ of each grid cell was calculated based on the observations in that cell and in relation to the observations in the cells already selected. If there were two or more cells with the same value, one was selected at random. Hence, this procedure can lead to slightly different results for each run.

Model validation

We focused our model evaluation on the area under curve (AUC) using receiver operating characteristic (ROC) analysis[38], which is a measure generally accepted for evaluating distributional model performance and that has been employed in recent comprehensive evaluations[39]. ROC AUC, however, provides a threshold-independent measure of model performance compared to that of null expectations and as such should provide an overall picture of the predictive nature of models[40]. To permit visualization of patterns of *P. santalinus* ecological niche variation, we combined the input environmental grids with the final ENM to create a new grid with a distinct value for each unique combination of environments. We exported the attributes table associated with this grid in ASCII format for exploration in a graphics program.

Results and discussion

Predictions of the distribution of *P. santalinus* were good and coincided well with the known distribution of the species (Figure 3). However, Maxent models inclined to be somewhat under-predicted. The GARP and BIOCLIM predictions on the other hand, were observed to be more extensive. As of today, this species has been reported only from the dry deciduous forests of the southern part of the Eastern Ghats; particularly in the districts of Kadapa and Chittoor. AUC scores for these models were 0.88 for Maxent, 0.850 for GARP and 0.750 for BIOCLIM. HP analysis explains the predictor variables and their independent and joint effects influencing the dependent variable; in this case, the presence/absence of the species. Of all the variables isothermality, temperature annual range and temperature seasonality had the greatest independent effects; other variables showed joint effects and together these variables explained much of the variability in the system (Figure 4).

P. santalinus predictions coincided well with the known distribution of the species. It has never been documented as native in the regions of the Eastern Ghats. AUC scores for these models paralleled the results of the previous surveys[2,39]. A value of –0.88 for Maxent, compared to 0.850 for GARP and 0.750 for BIOCLIM, suggests that Maxent is a better predictor than the other models (Figure 5). As such, the results of challenging models with predictions across densely sampled landscapes are seen to parallel those of previous comparison[39]. Results from the Maxent model seem to have

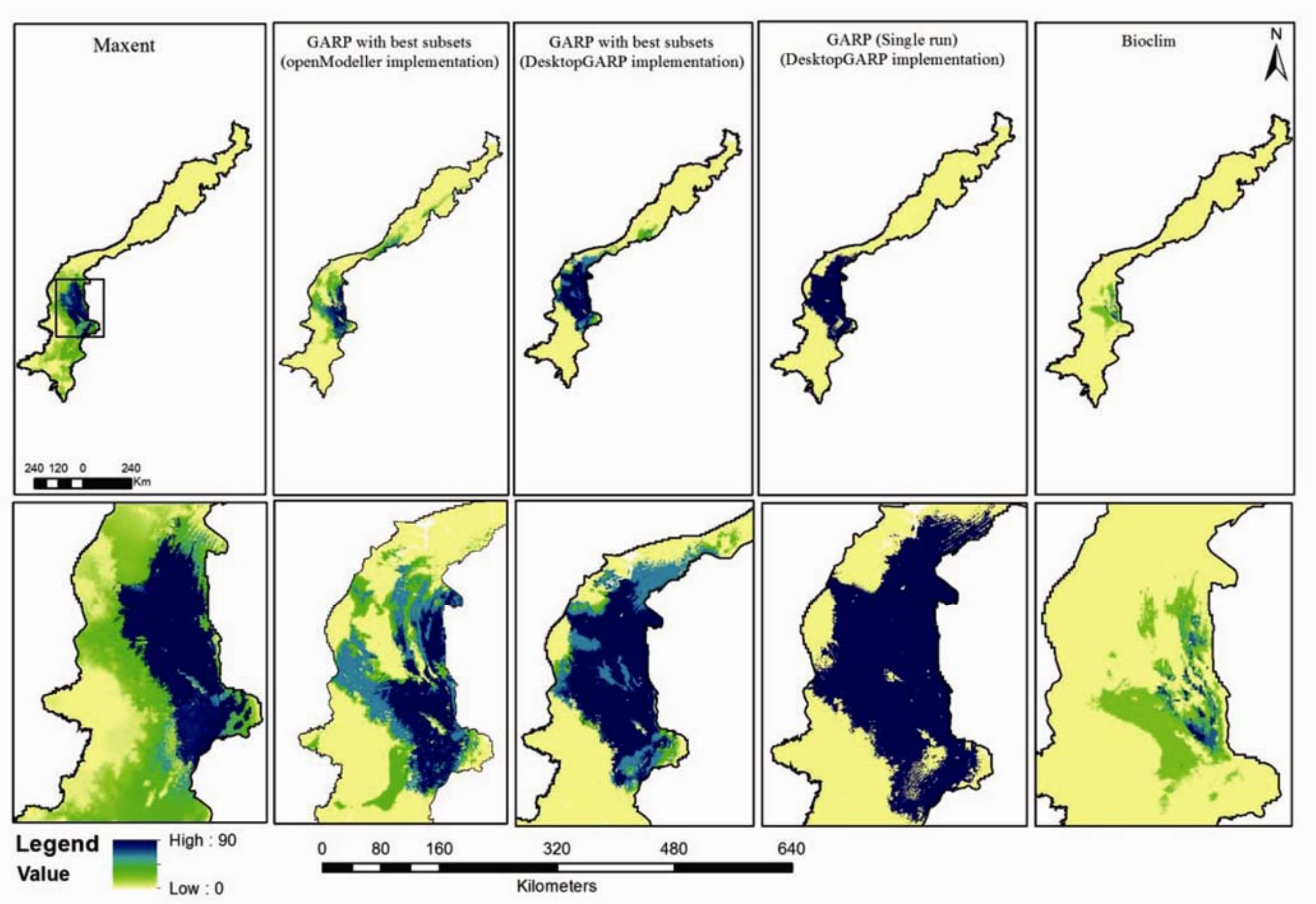

Figure 3. Coarse and close view of the predicted distribution analysed using multiple ecological niche models for the *P. santalinus* species.

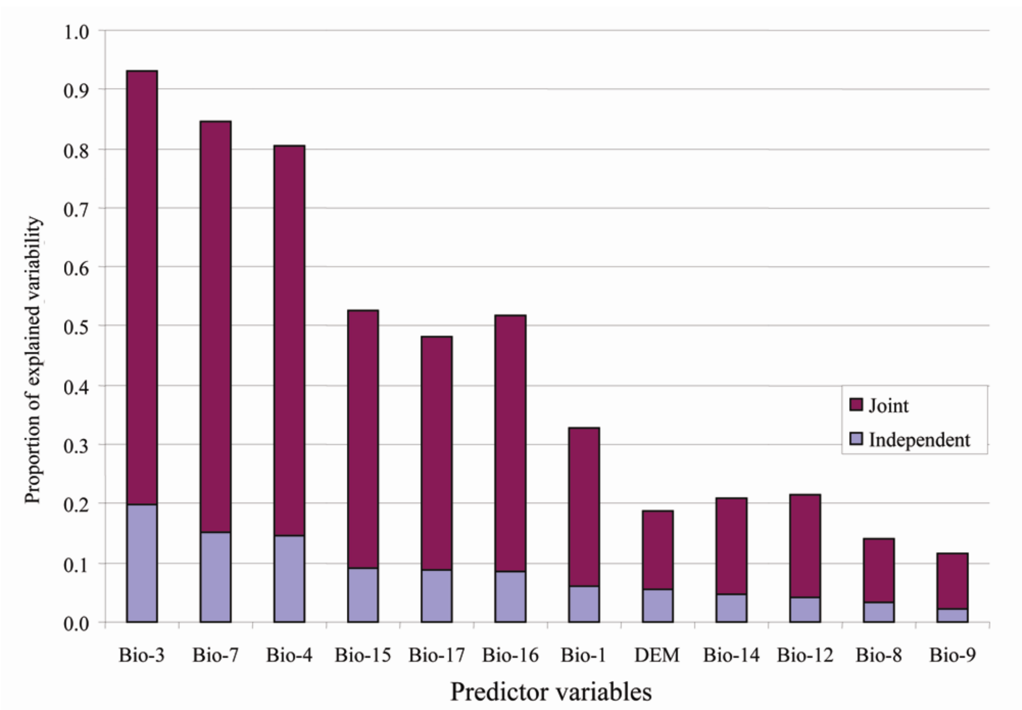

Figure 4. Proportional explained variability of predictor variables for the *P. santalinus* species.

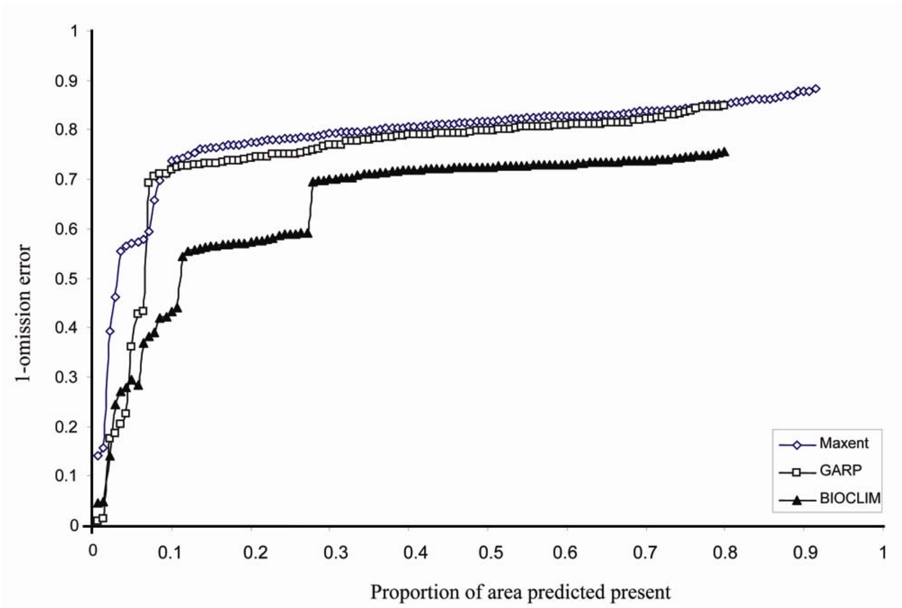

Figure 5. Model evaluation on area under curve using relative operating characteristics.

maximal accuracy level, may be due to its regularization procedure that counteracts a tendency to over-fit models. Our observations coincide with recent studies from the NCEAS model comparison that ranked GARP among the poorest performing of all algorithms and Maxent among the best[39]. Stockwell and Peterson[40] also found that Maxent achieved better predictive success rates, particularly at small sample sizes, and Phillips *et al.*[36] also found that the Maxent outperformed GARP, at least as evaluated using ROC AUC approaches.

Niche model predictions are supported by recent results from the research on ecological niche characteristic in the southern parts of the Eastern Ghats[41]. The model species affect the accuracy potential of the model, where species are widespread in both geographic and environmental space, and are generally more difficult to model than those with compact spatial distribution[42–45]. Other possible explanations for variation in model performance not related to geographic range size or ecological niche breadth are that some species are just not suited for climatic modelling and/or the spatial grain (pixel resolution), and are thereby inappropriate for modelling the distribution of some taxa in the study area of the Eastern Ghats. Other input variables like geology and disturbance might yield better prediction of *P. santalinus*. These results may differ for different study areas, at a different spatial scale (extent and/or grain), with varying qualities of model data (species and environmental), and for the study species of different ecological characteristics. Our results clearly indicate that future studies should use multiple evaluation measures, because each measure provides only a portion of the elusive 'truth' of the predictive ability of a species distribution model. In general, practitioners should remember that models are simply an estimate of the potential distribution of a species. Species distribution modelling cannot replace fieldwork intended to collect more distributional data, but can be a useful tool for data exploration to help identify potential knowledge gaps and provide direction to fieldwork design[43].

For the 19 bioclimatic and physiographic variables, we removed seven highly correlated, redundant variables, and then developed bivariate plots to summarize the distribution of species (Figure 6). These explorations reveal a narrow niche (even against the already specialized conditions of the southern Eastern Ghats) for the species-restricted to areas preserving narrow ranges of isothermality (4.7–5.4) and temperature annual range (19–22°C). Both topography (< 900 m) and annual precipitation (400–1100 mm) have no correction on its present occurrence and these surrogates exist as a broad range. Further, the mean temperature of both the wettest and driest quarters explains the narrow niche in relation to the entire Eastern Ghats.

Conservation implication

We observed three distinct clusters of *Pterocarpus* communities in 21 transects plots (Figure 7). The first cluster represents pure colonies of *Pterocarpus* and in the second cluster, it is mainly associated with *Anogeissus* and *Chloroxylon*. In the third cluster, the population mainly comprises other associate species like *Hardwickia*, *Ziziphus*, *Ochna*, *Garcinia* and *Strychnos* along with *Pterocarpus*. It also includes a secondary cluster, as given in Table 1. This species is becoming endangered primarily due to anthropogenic disturbances (logging, fire and non-timber forest produce collection) rather than natural processes. In past decades, this species was being

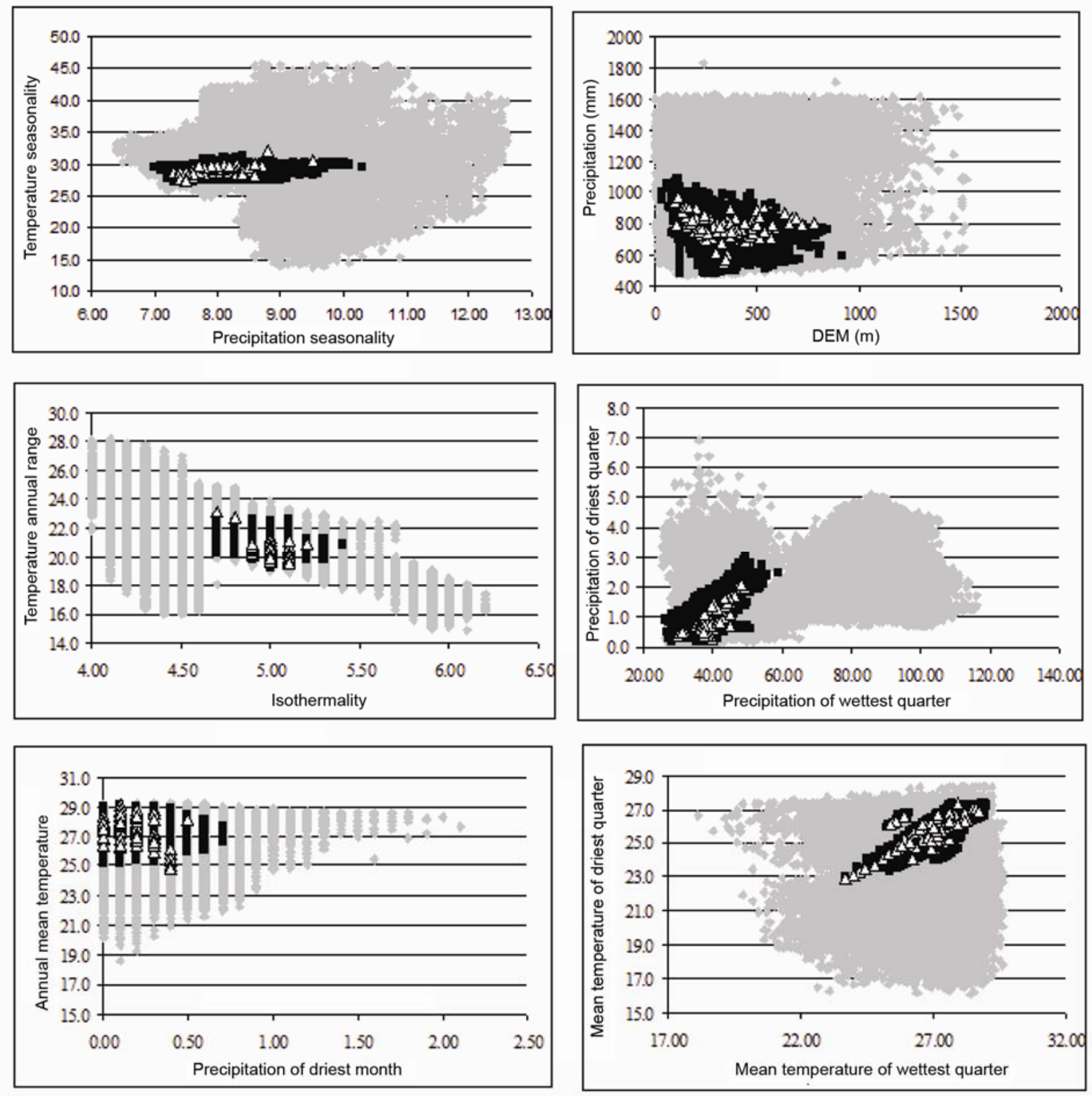

Figure 6. Exploratory visualization of *P. santalinus* L. niche in environmental space based on bioclimatic and physiographic variables (left to right: 1, Temperature seasonality versus precipitation seasonality; 2, Precipitation versus DEM; 3, Temperature annual range versus isothermality; 4, Precipitation of driest quarter versus precipitation of wettest quarter; 5, Annual mean temperature versus precipitation of driest month; 6, Mean temperature of driest quarter versus mean temperature of wettest quarter). Grey, Eastern Ghats condition; Black, Predicted area; White, Species location.

Table 1. Cluster analysis showing primary and secondary associations of *Pterocarpus* communities

Cluster	Primary association	Secondary association
1	Pure colonies of *P. santalinus*	
2	*Pterocarpus* with	*Anogeissus latifolia–Chloroxylon swietiena*
3a	*Pterocarpus* with	*Hardwickia binata–Ziziphus xylopyrus*
3b	*Pterocarpus* with	*Dolichandrone atrovirens–Ochna obtusata–Gardenia gummifera–Strychnos potatorum*
4	*Pterocarpus* with	Mixed associations (*Buchanania lanzan*, *Xylosma longifolium*, *Terminalia alata*, *Albizia amara*)

used both for its medicinal and hardwood purposes and was being heavily logged. As a result, there has been large-scale degradation in many of the pure colonies of *P. santalinus* with poor regeneration. During the survey, we observed many influxes of non-indigenous species (*Lantana*, *Chromalaena* and *Hyptis*) in context-dependent interactions like competition, which could alter the ecological function. Thus, anthropogenic disturbances

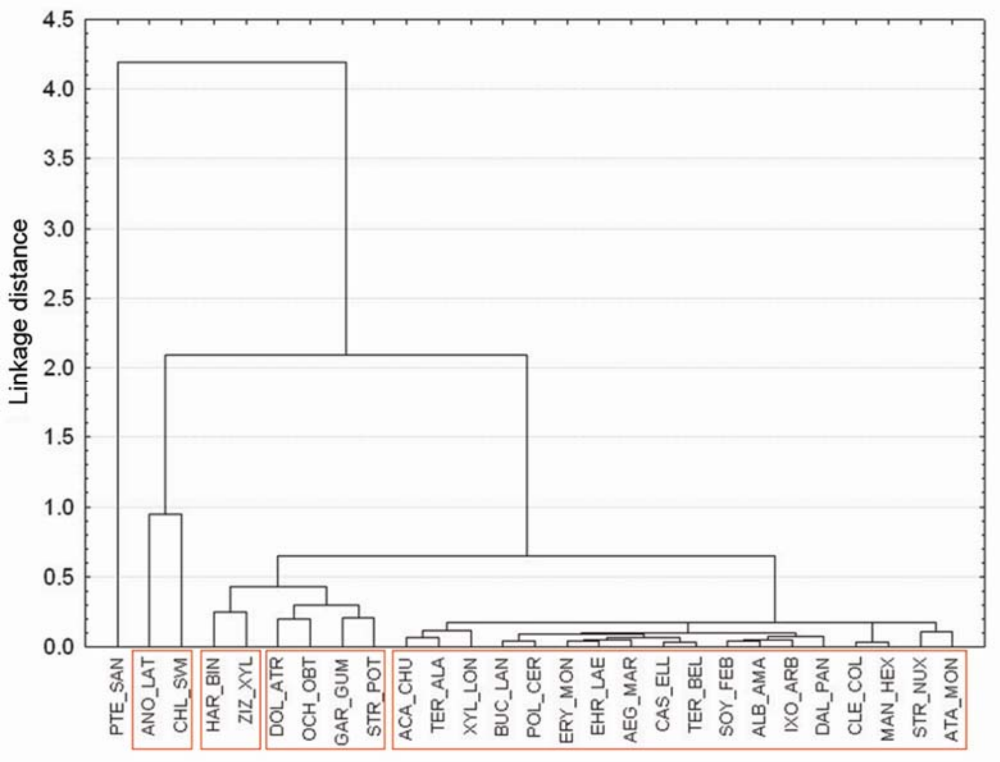

Figure 7. Cluster dendrogram showing the *Pterocarpus* communities in Kadapa District, Southern Eastern Ghats, Andhra Pradesh.

have a profound influence on environmental change[45] and alter environment of the native species, thereby endangering the habitats of the *P. santalinus*. The conservation action plan for any species or ecosystem is meant for minimizing the threat and reducing the vulnerability of the species. For *P. santalinus*, the prescriptions could be to develop a database on target species, monitoring population dynamics, minimizing the threats, extending the range of species and creating awareness.

Conclusions

In recent years, climate change has become a popular research topic because of its immediacy, and the profound effects it has on natural systems and society. Rapid development of biodiversity informatics tools has stimulated research focused on forecasting climate-change impacts on biodiversity. ENM has become particularly important, because it provides one of the few predictive approaches to understanding the geographic dynamics of species. Currently, it is impossible to identify any single modelling algorithm that performs better than all others for all types of species and data conditions, and we visualize that the use of multiple methods may prove to be the most robust current option. From our studies it is clear that ENM is a useful tool in outlining and understanding the distribution in ecological and environmental space, and may prove useful in a variety of biodiversity applications that require detailed information about geographic distributions of species, particularly in the changing climate. Future steps need to include data on demography, structural and functional pattern, its threat status to develop detail conservation action plan.

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