



Integration of community ecology and habitat suitability modelling for restoration and conservation of two endemic tree species from the Western Ghats, India

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Abstract

Key message The recurrent anthropogenic disturbances, poor regeneration potential, high carbon stocks, and restricted habitat suitability warrants effective conservation and restoration of two ecologically and economically important endemic tree species.

Abstract Despite a growing consensus on the application of species distribution models (SDM) in predicting species distributions, the integration of community ecology of endemic species based on field studies with SDM is largely an isolated area of research. This paper presents a detailed account of the distribution, habitat preferences, population ecology and biomass of two endemic tree species, *Terminalia paniculata* Roth and *Lagerstroemia microcarpa* Wt. from 119 (0.1 ha) plots sampled in the Shettihalli landscape of the central Western Ghats, India. MaxEnt SDM was used to predict their distribution by testing the influence of environmental factors. We found a significant difference in the density, basal area and carbon stocks of *T. paniculata* across the dry and moist deciduous and semi-evergreen forests ($p < 0.05$). Both species were found to be predominant in moist deciduous forests and contributed high biomass carbon. The regeneration potential of *T. paniculata* was poor in dry deciduous and semi-evergreen forests, whereas *L. microcarpa* displayed poor to no regeneration in all the forest types. Further, SDM predicted a high probability of distribution for both species. The main factors driving the occurrence in Shettihalli were land use and land cover, precipitation amount of the driest month, soil pH and elevation. The current high suitability of *T. paniculata* and *L. microcarpa* were around 137.66 km² and 120.49 km², respectively. Variations in the population structure and regeneration in different forest types are attributed to ongoing anthropogenic disturbances in the landscape. The findings of this study can be extremely helpful in developing proper conservation strategies to protect these species and restore their habitat. We highly recommend the incorporation of SDMs in conservation studies.

Keywords Biomass · *Lagerstroemia microcarpa* · MaxEnt · Regeneration · Species distribution modelling · *Terminalia paniculata*

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Introduction

Over the last few decades, there has been a dramatic decline in biodiversity in natural ecosystems due to population growth, changes in land use, over-exploitation of forest resources and biological invasions (Ripple et al. 2017; Díaz et al. 2019). In addition, climate change has taken centre stage as a major disruptor of local biodiversity, causing phenological variations (Visser and Both 2005), changes in species assemblages (Steinbauer et al. 2018), negative effects on species diversity and ecosystem functioning (Belle et al. 2016; IPCC 2018); as well as range contractions leading to population decline (Bush et al. 2020). Consequently,

species across all taxonomic groups are facing the sixth mass extinction (McCallum 2021), with every two out of five plant species being threatened globally (Antonelli et al. 2020). Regarding this in-situ conservation of tree species (the dominant life-forms) within natural reserves and protectorates is a popular remedy to reduce extinction risks and achieve species recovery (Deguise and Kerr 2006). Recent scientific recommendations for a Global Deal for Nature call for protecting at least 30% of lands by 2030, with an extra 20% of lands set aside as regions for climate stabilization (Dinerstein et al. 2019). Moreover, increasing the area under a protective cover and conserving biodiversity is important for countries to comply with and achieve the goals of multiple international policies such as the United Nations Sustainable Development Goals (UN SDGs), UN Agenda 2030, and Convention on Biological Diversity (UNEP-WCMC, IUCN, NGS 2018).

Considering this dire scenario, global biodiversity hotspots with high species richness and endemism are at high risk of extinction (Chitale et al. 2014). India has a rich biodiversity that accounts for 11% of the world's flora, with 33% of the angiosperms occurring in the country being endemic to the region (Singh et al. 2015; Singh and Chaturvedi 2017). However, increasing human population density has put undue pressure on these delicate eco-regions (Ramesh and Gurukkal 2007). The Western Ghats is one such vulnerable landscape which has undergone a forest cover loss of 35.3% from 1920 to 2013 (Reddy et al. 2016). Despite this, only 9% of its forest area falls under the protected area network (Chitale et al. 2014). Over the years, several authors have raised the importance of conserving endemic plant species to protect this heterogeneous landscape (Ramesh and Pascal 1997; Myers et al. 2000; Ramesh and Gurukkal 2007).

The moist deciduous forests of the Malnad region of Shivamogga in central Western Ghats are blessed with important timber and non-timber forest product species of great cultural, social and economic values. Among these, *Terminalia paniculata* and *Lagerstroemia microcarpa* are two tree species known for their timber value, durability and medicinal properties (Bhusnure et al. 2009; Pillai and Hrideek 2018; Bhat 2020). These species have dominant populations in deciduous forests of the Western Ghats and are endemic to the region (Sukumar et al. 1992; Ramesh et al. 2010). In the past, large tracts of deciduous forests were heavily exploited for timber, but regeneration of the species was considered good despite their ongoing harvest (Troup 1921). Currently, the forest cover in Shivamogga district (including Shettihalli) has declined by 21.5% because of land clearance for the implementation of reservoirs, roads, plantations and hydroelectric projects (Ramachandra et al. 2013). Extensive extraction of wood, illegal logging in the past and disturbances through unmanaged anthropogenic activities during the recent times have put these species

under a vulnerable stage and may lead to local extirpation (Babu et al. 2023a). More recently, Nair et al. (2002) and Pillai and Hrideek (2018) reported poor regeneration and germination potential, which raised concerns for the long-term sustenance of these endemic species in the Western Ghats.

In the given context, Shettihalli wildlife sanctuary (SWS), a human-dominated landscape and adjacent reserve forests in the Shivamogga district were considered suitable sites based on a preliminary survey by Babu et al. (2021). They form dominant populations in the landscape and have voluminous trees with widespread occurrence in the three forest types: dry, moist deciduous and semi-evergreen, despite the considerable portions of the landscape exploited for timber. The native population of these species are declining due to various anthropogenic perturbations coupled with extremely low regeneration. The presence of many villages, enclosures and frequent forest fires inside the landscape has further exacerbated the situation and have threatened the tree population. To secure the persistence of these endemic plant species in the face of rising challenges to plant diversity, a sound understanding of the essential indicators, i.e. ecology of a species, their interactions, phenology, plant functional traits, regeneration status, successional process, resource use, environmental services such as carbon stocks and sequestration etc. are necessary (refer to Evangelista de Oliveira et al. 2021; Chaturvedi et al. 2021). These indicators have been proven to be successful in choosing potential species in ecological restoration (Siddig et al. 2016; Zhang et al. 2022). Additionally, information on forest demography plays a crucial role in sustaining the specific species population at present, further strengthening the process of regeneration and recruitment of future populations at the landscape scale (Ashton et al. 2018). From a management perspective, knowledge of the aforementioned ecological factors is required to formulate the necessary prerequisites for protecting a species' population and preventing its decline.

To successfully reintroduce or rehabilitate and protect a species in an ecosystem, a thorough knowledge of the potential distribution of the species and its habitat requirement is essential. To achieve this, new and innovative approaches are required. Habitat suitability modelling is one such method that can be used with limited conservation resources and manpower in areas with high habitat suitability so that a species can be protected more effectively (Rather et al. 2022). Several modelling techniques were being developed, which have promoted the use of species distribution model (SDM). There has been widespread use of SDMs in the field of ecology (He et al. 2015) as well as conservation biology as a method to predict conservation hotspots for endemic species (Rather et al. 2022), including restoration ecology as a method to restore ecosystems in general (Banerjee et al. 2021). The maximum entropy model or MaxEnt, is a well-known SDM technique that is widely accepted for

its effectiveness in modelling species distributions. (Phillips et al. 2006; Almarinez et al. 2021). It is a robust model based on an ecological niche machine-learning algorithm (Guisan et al. 2007) and can be used for species with small sample sizes (Wisn et al. 2008; Hale 2021).

To date, there are only a few studies in the literature that address the population ecology, regeneration and habitat distribution modelling of endemic, rare and ecologically important species (Adhikari et al. 2012; Shaltout et al. 2015; Paul et al. 2019; Iralu et al. 2020; Singh et al. 2021; Rather et al. 2022). Moreover, studies on the autecology of endemic species are also limited and poorly understood (Valappil and Swarupnandan 1996). It is essential to have in-depth information about an individual species to predict its behaviour and population at the landscape level. Such ecological studies, at the species level, help us gain complex insights into the emergent properties of the ecosystem (Odum and Barrett 2005). Therefore, in data-deficient regions, insights from SDM combined with community ecology at the local-spatial scale can aid in formulating effective restoration strategies. As far as we know, no studies were attempted to study the ecological attributes and modelled the distribution of the focal species. Yet, such scientific knowledge is crucial for successfully directing restoration initiatives to conserve these endemic species. Against this backdrop, we undertook this study to advance ecological knowledge and assist in conservation decision-making for *T. paniculata* and *L. microcarpa* in the Western Ghats biodiversity hotspot. Specifically, we asked the following key questions: (1) What are population structure and carbon stocks across the forest types and the landscape? and do they differ among the forests? (2) What is the regeneration status of these species? (3) What is the distribution pattern (suitability) of the species, and what factors exhibit such a pattern? (4) How well-managed are these species currently, and what are the principal threats to conservation and recommendations for protection? and finally (5) How can the information on species association, regeneration, and SDM be guided to restore these species effectively on the ground?

We hypothesized (H1) that the population structure and carbon stocks significantly vary among the different forests for the selected species which are driven by physiognomy and environmental factors (Ramesh et al. 2010; Magesh 2014). We also hypothesized (H2) that there are significant differences in the regeneration status of both the species in different forest types and their recruitment is explained by prevailing anthropogenic pressures and low regenerative potential (Pillai and Hrideek 2018; Valappil and Swarupnandan 1996). Thirdly, the habitat suitability of the two species is explained by a combination of (H3) specific environmental or ecological factors. Lastly, (H4) information on ecology, species association, regeneration, and SDM significantly contributes to the identification of priority regions for effective conservation and restoration of these species.

Materials and methods

Study site

The present study was undertaken in SWS and the adjoining territorial forests of the Shettihalli landscape (Shettihalli; 13°42′—14°01′N; 75°14′—75°34′E); part of central Western Ghats, spatially spread over 750 km² (Fig. 1). Topographically, Shettihalli has contrasting elevated landforms, with varying elevations across the eastern (600 m) and western regions (850–1050 m). The microclimatic conditions and orographic effect of the Western Ghats on the region cause it to experience variable rainfall (1044–3076 mm) and temperature (Min: 17.50–19.38 °C and Max: 27.76–29.92 °C; Hijmans et al. 2005; Babu et al. 2021). According to Champion and Seth (1968), the following forest types predominate in SWS: (1) Southern tropical semi-evergreen forest (2A/C₂), (2) Southern tropical moist deciduous teak-bearing forest (3B/C₁) [Sub-type: Moist teak forest (3B/C_{1b})], (3) Southern tropical moist mixed deciduous forest (3B/C₂), and (4) Southern dry mixed deciduous forest (5A/C₃). Two hundred sixty-nine species of woody flora were reported from these forest types, which belonged to 68 diverse families (Babu et al. 2021). Based on petrological and pedological studies, the landscape has a diverse complex of geological formation of the Archean type, dominated by gneisses and granites. The soil is acidic in nature ranging from medium to high and is classified into ferrallitic soils and lithosols (Bourgeon 1989). The landscape has a human populace, with significant enclosures and villages adjacent to the vegetated areas with well-connected road networks (Anonymous 2005; Babu et al. 2023a).

Study species

Terminalia paniculata Roth (Fig. 2b–e) is a moist deciduous tree species of the family Combretaceae, endemic to peninsular India. It is an important timber species and a hardwood tree commonly found in the Western Ghats. In tropical and subtropical moist broadleaf forests, the genus *Terminalia* is represented by 100 species worldwide and providing beneficial ecosystem services in the form of timber, NTFP, tannins and medicinal compounds (Pillai and Hrideek 2018). In the Western Ghats, *T. paniculata* is found in the semi-evergreen, moist teak-bearing forests, moist mixed deciduous and dry deciduous forests and associated with the floristic compositions of the type *Lagerstroemia microcarpa*—*Tectona grandis*—*Dillenia pentagyna* and *Anogeissus latifolia*—*Tectona grandis*—*Terminalia alata* (Champion and Seth 1968; Pascal 1986).

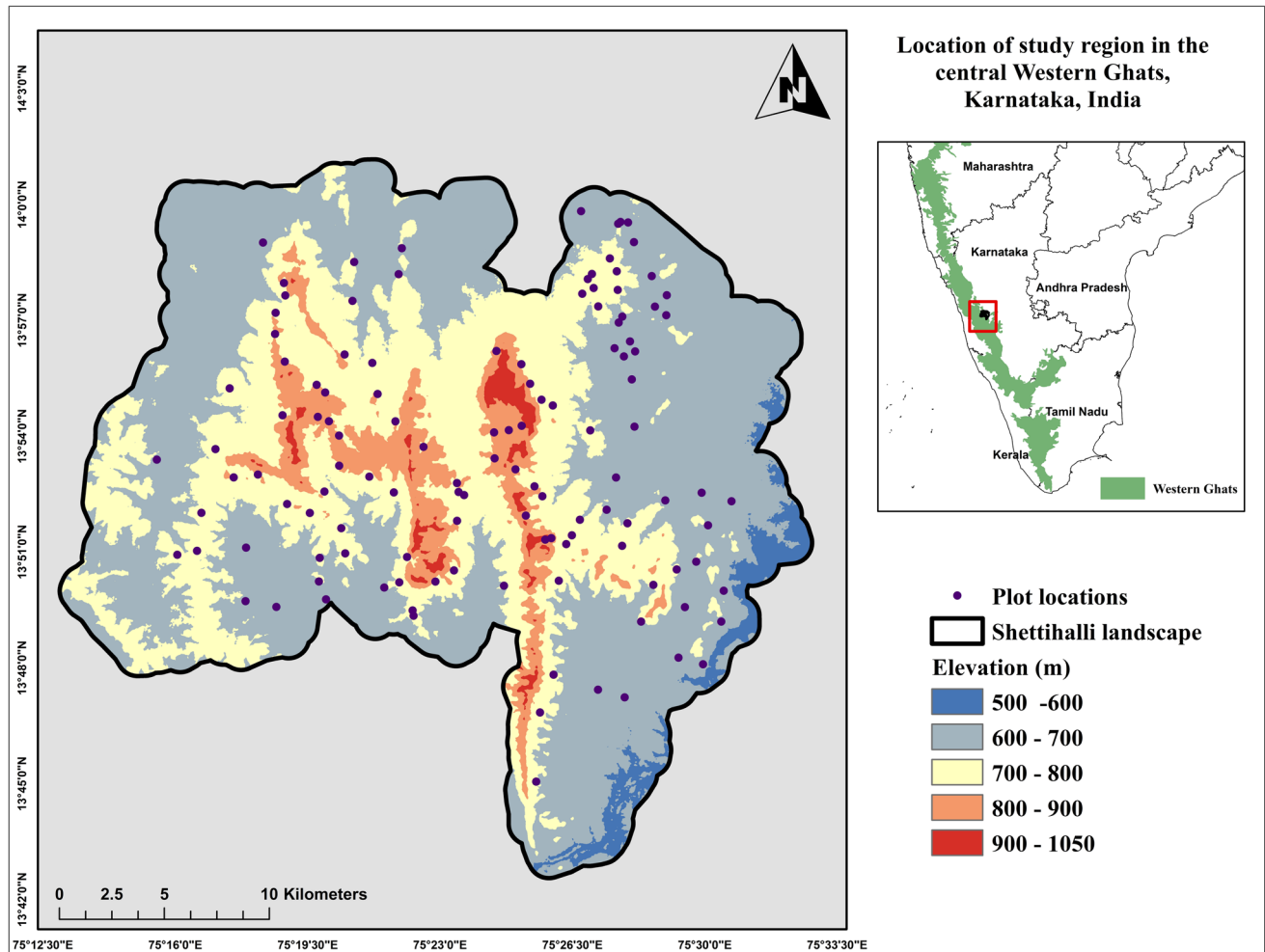


Fig. 1 Location map of Shettihalli landscape and the distribution of sample plots (the dots) in the central Western Ghats, Karnataka, India

It grows well in the mean temperature range (22–39 °C) and at the elevation up to 1200 m. In literature, it is commonly known as ‘Kindal’, and in Shettihalli, it is referred as ‘Honalu’. The tree’s height varies between 15–30 m; it flowers and fruits between July–December, and the leaves (20 × 10 cm) are elliptic-oblong (Fig. 2c, with an acute apex and cordate base. The flowers are white (Fig. 2d) in large panicles, and the fruit is unequally winged with brownish-red colour (Fig. 2e; Bhat 2020).

Lagerstroemia microcarpa Wt. (Fig. 2f–j) is a codominant species with *T. paniculata* commonly referred to as ‘Ben-teak’ and locally called ‘Nandi’. It occupies the same eco-regions as other moist deciduous species and has about 80 species in the genus belonging to Lythraceae (Roy et al. 2019). In Karnataka, Tamil Nadu and Kerala, this hardwood timber species is restricted to the Western ghats at an elevational range of 400–1000 m and a mean temperature range of 17–46 °C (Troup 1921; Nair et al. 2002). The associated floristic composition for *L. microcarpa* is identical to that

of *T. paniculata* (Pascal 1986); the tree grows in the range of 20–30 m height, and it flowers during May and July and fruits in November–December (Nair et al. 2002). The leaves (6–10 cm) are elliptic–ovate, ovate-lanceolate, with an acute apex and hoary tomentose beneath (Fig. 2g). The flowers are white in terminal panicles (Fig. 2h) and the fruit capsule ellipsoid (1.8 cm; Fig. 2i, j; Bhat 2020).

Sampling and data collection

For enumerating the population structure, regeneration, and biomass of *T. paniculata* and *L. microcarpa*, both at the forest type and the landscape level, a total of 119, 0.1 ha (31.63 m × 31.63 m) square plots were established by stratified random sampling. Plot selection was based on the topography, climate, canopy density and forest type of the study area. Random points were generated in the ArcGIS environment keeping 500 m as the minimum distance between the plots assuming that the maximum portion of

the landscape is covered. Geolocations of each plot were recorded using a hand-held Garmin 66SR GPS unit in the field. In Moist deciduous forests (MDF)—72, Dry deciduous forests (DDF)—25 and Semi-evergreen forests (SEF)—22 plots were established. Within each plot, the girth at breast height (GBH) of individual live trees of the study species ≥ 30 cm was measured at 1.3 m from the ground. Trees with multi-stems were measured separately, and for those trees with buttresses, GBH was measured above the standard height of 1.3 m. To determine the regeneration potential, saplings > 3.1 cm and < 30 cm were counted in two diagonal 10 m \times 10 m sub-quadrats within the 0.1 ha plot; also, the seedling (≤ 1 m tall) counts were taken from five 1 m \times 1 m sub-quadrats placed at each corner and centre of the plot. Additionally, the predominant species occurring inside the plot were also noted to derive species associations. Species identification was made in the field with the help of domain experts with at least 10 years field experience and the voucher specimens were cross verified with the herbarium records at Herbarium Institut Français de Pondichéry (HIFP; <https://www.ifpindia.org/resources/herbarium/>).

Data analysis

Density and basal area

The density of the species for the forest types: MDF, DDF and SEF was computed using the Eq. (1).

$$\text{Density}(D) = \frac{\text{Total number of individuals of tree species}}{\text{Area}} \quad (1)$$

Similarly, we computed the basal area of the species for all three forest types by converting the GBH (cm) to DBH (m) and applying it to Eq. (2).

$$\text{Basal area} = 0.7854 \times D^2, (D = \text{DBH in m}) \quad (2)$$

Biomass estimation

The field data (DBH) obtained from the plots was applied to the species and region-specific volumetric equations (Table 1; FSI 1996) to get the tree volume of the individual trees ≥ 10 cm DBH. The subsequent volume obtained was multiplied by the species' wood-specific gravity to give the tree's merchantable timber biomass. Further, species and regional-specific biomass equations (Table 1; FSI 2012) were applied to estimate the individual tree's branch and foliage biomass. The merchantable biomass, branch and foliage biomass were summed to give the aboveground biomass

(AGB) of the individual tree of the respective species. Further, belowground (BGB) was computed using the allometric equation given by Cairns et al. (1997).

$$\text{BGB} = \exp[-1.059 + 0.884 \times \ln(\text{AGB}) + 0.284] \quad (3)$$

The total biomass (TB) for the species was computed by summing AGB and BGB. A conversion factor of 0.5 (50%) multiplied by TB was used for the calculation of the tree biomass carbon (TBC) of the individual tree species (Metz et al. 2005).

Regeneration

The regeneration of the concerned species was studied in all three forest types separately. The collected data were categorized into seedlings, saplings and adults for both the species and their densities were taken into account to determine the regeneration status proposed in the existing literature (Khan et al. 1987; Shankar 2001; Buragohain et al. 2023).

Statistical analysis

The data were initially subjected to the Shapiro–Wilk test for normality. A one-way ANOVA was performed to test the statistical difference between the forest types for the variables (density, basal area and TBC). We used Tukey's post hoc test for a pairwise (forest-type) comparison of the above variables. All the statistical analyses were performed in R 4.2.1 (R Core Team 2021).

Community association

To examine the species association, the presence-absence matrix of occurrence data from the pooled dataset (119 plots) was visualized using the probabilistic co-occurrence model implemented in the 'Cooccur package' (Griffith et al. 2016) in R which uses hypergeometric approach (Veech 2013).

Habitat suitability modelling

Occurrence data and spatial autocorrelation

The Shettihalli landscape of central Western Ghats was found suitable for performing species distribution modelling (SDM), with the occurrence of optimal populations of *T. paniculata* and *L. microcarpa*, from the studied 119 plots. Additionally, occurrence data were also collected from the field survey of the landscape, with each point (with at least five individuals grouped) geotagged using a GPS device (Garmin 66SR). The total occurrence data used for the habitat suitability modelling (HSM) are 203 for *T. paniculata*

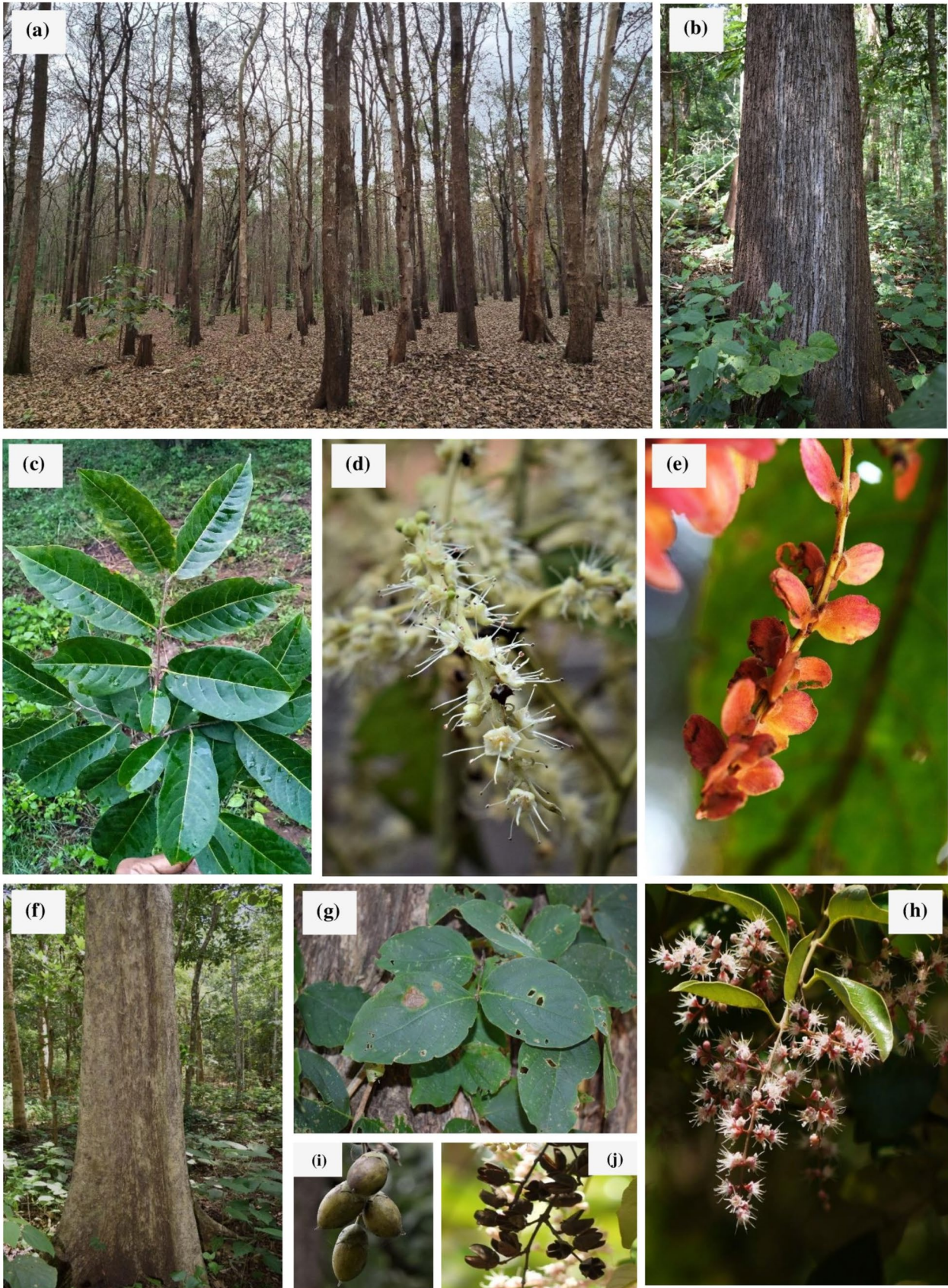


Fig. 2 Characteristic features of *Terminalia paniculata* and *Lagerstroemia microcarpa* in Shettihalli. (a) Inner stand view of the study species with relatively no understorey and disturbance; (b) Image of the *T. paniculata* bark and bole; (c) A close-up of leaf twig of *T. paniculata*; (d and e) A close-up of flower and fruit of *T. paniculata*; (f) Image of the *L. microcarpa* bark and bole; (g) Phyllotaxy of *L. microcarpa*; (h) A close-up of flowers of *L. microcarpa* and fruits (i and j)

and 168 for *L. microcarpa*. We used the ‘spThin’ package (Aiello-Lammens et al. 2015) in R 4.2.1 (R Core Team 2021) to spatially rarify the occurrences: we ran 100 thinning replicates for the occurrence data with 1 km as the minimum allowed distance between two thinned occurrences, to eliminate clustering of presence points within adjacent raster cells of environmental predictors (Sreekumar and Nameer 2022).

Environmental predictors (layers/covariates)

Environmental predictors are essential in determining species’ presence and distribution across the landscape (Remya et al. 2015; Agwu et al. 2020; Hazarika et al. 2023). Land use and land cover (LULC) was created using supervised classification of Sentinel-2 level 1C Ortho-rectified, cloud-free satellite imagery of 10 m resolution data downloaded from the Copernicus open access hub (<https://scihub.copernicus.eu/>) for December 2020 (Babu et al. 2023b). Regarding the climate, 19 bioclim layers and three physiological variables (Gardner et al. 2019), i.e. growing season length (GSL), growing season precipitation (GSP) and growing season temperature (GST) were extracted from the CHELSA-BIOCLIM + database (https://envdat.ch/#/metadata/bioclim_plus; Brun et al. 2022) at 1 km² resolution. Additionally, edaphic factors: pH, soil organic carbon (SOC) and nitrogen were retrieved from SoilGrids (<https://soilgrids.org>; Poggio et al. 2021) at 250 m resolution, and topographic features: slope and elevation were extracted from Shuttle Radar Topographic Mission (STRM GL1) data (<https://opentopography.org/>) at 30 m resolution. The resolution of all the environmental layers was adjusted to 10 m using ‘resample’ function in ArcGIS v. 10.2 environment.

Multicollinearity test

Taking into cognizance of the selected predictors before applying to the MaxEnt model, variables were subjected to the variance inflation factor (VIF) test to determine the multicollinearity among them by using the R package ‘usdm’ (Naimi 2017). Firstly, the 19 bioclim and three physiological variables were tested for multicollinearity, which resulted in 12 variables with collinearity issues (VIF > 10, Gaisberger et al. 2022) that were eliminated from further analysis. Subsequently, seven climatic variables with other topography, LULC and edaphic variables were considered based on the

spatial extent and ecology of the species across the forest types in the landscape. These include LULC, elevation, slope, soil organic carbon (SOC), pH, nitrogen, mean diurnal air temperature (BIO2), isothermality (BIO3), temperature seasonality (BIO4), mean daily maximum air temperature of the warmest month (BIO5), annual range of air temperature (BIO7), precipitation amount of the driest month (BIO14) and growing season length (GSL). These environmental variables were further filtered to reduce the amount of redundant information and improve the prediction accuracy of the model.

MaxEnt modelling

The habitat suitability modelling for *T. paniculata* and *L. microcarpa* was performed by employing the geotagged points (occurrence data) in confluence with the environmental predictors to the maximum entropy (MaxEnt) algorithm (Phillips et al. 2006; Warren and Seifert 2011) implemented in ‘sdm’ package of R (Naimi and Araújo 2016). The MaxEnt is a popular user-friendly machine-learning algorithm widely acknowledged in modelling rare, endemic and ecologically important species, particularly with narrow distribution and small occurrence records (Elith et al. 2011; Namitha et al. 2022). Through the algorithm, we selected ten bins (folds) for our modelling with 1000 randomly generated background points (pseudo-absences) across the study area using the k-fold cross-validation method to partition presence into testing and training bins. The majority (70%) of the partitioned occurrence data of the study species was implemented for training the model, and the remaining (30%) was applied for testing and evaluating the robustness of the model (Agwu et al. 2020).

Model evaluation and habitat suitability map

The prediction of probability distribution and habitat suitability of the species in the landscape by the MaxEnt model requires an accuracy assessment to test its validity (Agwu et al. 2020). We computed the area under curve (AUC) and True skill static (TSS) to assess the model’s prediction reliability (Allouche et al. 2006). According to Hirzel et al. (2006), the AUC value thresholds consist from 0 to 1, with $AUC \geq 0.75$ representing closer to the best model (Agwu et al. 2020; Singh et al. 2021). In addition to the above, an additional performance indicator, Continuous Boyce Index (CBI; Boyce et al. 2002), was used to test the calibration accuracy of the model consisting of presence-only data of the species (Shitara et al. 2021). This metric is computed in R by the ‘ecospat’ (Di cola et al. 2017) package, which measures and differentiates the model’s ability to predict the probability distribution of the species from that of a random

Table 1 Volumetric/Biomass equations of *Terminalia paniculata* and *Lagerstroemia microcarpa* in Shettihalli landscape (Shettihalli), central Western Ghats, India

Sl. no	Species and wood density (WD)	Biomass equation	Type of biomass
1	<i>Terminalia paniculata</i> Roth	$BE_1 = 362.5509D^2 + 278.3135D - 17.7837$	Branch biomass
		$BE_2 = 8.1731D^2 + 10.4816D - 0.7031$	Foliage biomass
		$BE_3 = 0.2724D_1^2 - 0.0125D_1 - 0.0558$	Branch biomass
		$BE_4 = 0.0064D_1^2 - 0.0052D_1 + 0.0306$	Foliage biomass
		$V = 0.13100 - 1.87132D + 9.47861D^2$	Bole biomass
2	<i>Lagerstroemia microcarpa</i> Wt.	$BE_1 = -123.7223D^2 + 290.7752D - 13.5650$	Branch biomass
		$BE_2 = -2.7947D^2 + 7.1714D - 0.3286$	Foliage biomass
		$BE_3 = 0.2400D_1^2 - 0.1514D_1 + 0.7339$	Branch biomass
		$BE_4 = 0.0041D_1^2 - 0.0095D_1 + 0.0495$	Foliage biomass
		$V = 0.23839 - 2.48071D + 10.14106D^2$	Bole biomass

(V) volume in m^3 , (D) dbh in m, (BE_1) branch biomass for tree dbh ≥ 10 cm, (BE_2) foliage biomass for tree dbh ≥ 10 cm, (BE_3) branch biomass for tree dbh ≤ 10 cm, (BE_4) foliage biomass for tree dbh ≤ 10 cm

Source: FSI (1996, 2012)

Table 2 Tree density, basal area, biomass carbon contribution of *Terminalia paniculata* and *Lagerstroemia microcarpa* in Shettihalli

Attribute	DDF		MDF		SEF		Landscape	
	<i>Ter pan</i>	<i>Lag mic</i>	<i>Ter pan</i>	<i>Lag mic</i>	<i>Ter pan</i>	<i>Lag mic</i>	<i>Ter pan</i>	<i>Lag mic</i>
Density (ha^{-1})	27.22 ± 5.59	16.67 ± 3.33	85.74 ± 6.62	42.34 ± 8.33	38.67 ± 5.42	24.55 ± 5.93	68.32 ± 5.26	37.87 ± 6.57
Basal area ($m^2 ha^{-1}$)	0.94 ± 0.21	0.26 ± 0.13	9.80 ± 0.92	4.18 ± 0.48	5.29 ± 1.20	4.97 ± 2.01	7.55 ± 0.73	4.13 ± 0.52
AGB ($Mg ha^{-1}$)	4.71 ± 1.11	1.45 ± 0.42	62.61 ± 6.39	21.25 ± 2.60	33.90 ± 8.34	27.60 ± 11.84	48.03 ± 5.00	21.42 ± 2.94
BGB ($Mg ha^{-1}$)	1.19 ± 0.27	0.40 ± 0.11	12.38 ± 1.15	4.44 ± 0.51	6.69 ± 1.51	5.21 ± 2.07	9.54 ± 0.92	4.38 ± 0.54
TB ($Mg ha^{-1}$)	5.91 ± 1.38	1.85 ± 0.53	74.99 ± 7.54	25.68 ± 3.10	40.59 ± 9.85	32.81 ± 13.91	57.57 ± 5.91	25.80 ± 3.48
TBC ($Mg ha^{-1}$)	2.95 ± 0.69	0.93 ± 0.26	37.49 ± 3.77	12.84 ± 1.55	20.30 ± 4.91	16.41 ± 6.95	28.78 ± 2.96	12.90 ± 1.74

AGB aboveground biomass, BGB belowground biomass, TB total biomass, TBC tree biomass carbon, DDF dry deciduous forest, MDF moist deciduous forest, SEF semi-evergreen forest, values indicate mean \pm SE

distribution model (Manzoor et al. 2020). For this index, the Spearman correlation coefficient varies from -1 to $+1$, where the values closer to 1 represent the model's prediction is certain and in line with presence-only data. The built-in function 'getVarImp' in 'sdm' package was used to determine the relative importance of each environmental variable (Elith et al. 2011). Further, the 'sdm' package facilitated the computation and visualization of response curves, which depict the relationship between the probability of species occurrence and each predictor variable. They show the variations in response associated with a specific environmental predictor, while holding all other predictors constant at their respective mean sample values. Finally, the prediction outputs were exported to the ArcGIS v. 10.2 environment and divided into four suitability classes, i.e. unsuitable, low suitable, moderately suitable, and highly suitable zones using the natural break method (Jenks 1967). This method is popular and highly recommended in SDM studies because of its ability to identify the break points by looking for patterns inherent in the data (Yang et al. 2023).

Results

Density and basal area

In MDF, the density of *T. paniculata* and *L. microcarpa* was the highest at 85 individuals ha^{-1} and 42 individuals ha^{-1} , which constituted the dominant forest type followed by the SEF (Table 2; Fig. 3). The representation of the study species in DDF was the lowest at 27 individuals ha^{-1} (for *T. paniculata*) and 16 individuals ha^{-1} (*L. microcarpa*). At the landscape level, the species dominantly occupy the upper stratum in all three forest types, represented by 68 individuals ha^{-1} and 37 individuals ha^{-1} , respectively. The density varied significantly across the forest types ($p < 0.05$; Fig. 3a) for *T. paniculata*. Tukey post hoc test also revealed a statistically significant difference ($p < 0.05$) between the pair groups (DDF vs. MDF and MDF vs. SEF). In the case of *L. microcarpa*, both ANOVA and post hoc tests showed no statistically significant difference across the forest types (Fig. 3d).

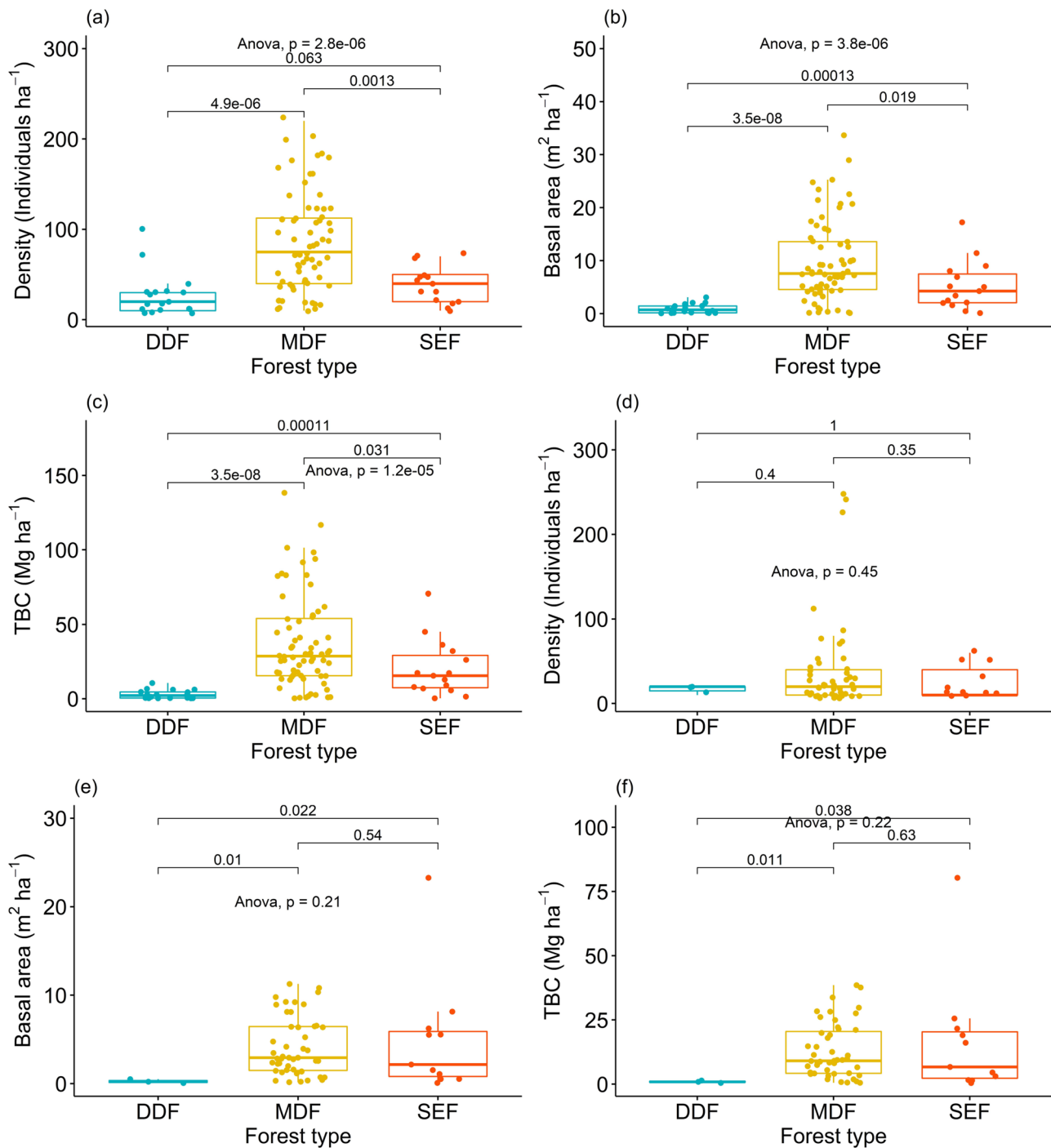


Fig. 3 Tree density, basal area and tree biomass carbon (TBC) distribution of *Terminalia paniculata* (a, b, c) and *Lagerstroemia microcarpa* (d, e, f) among three forest types (dry deciduous—DDF; moist deciduous—MDF; semi-evergreen—SEF) of Shettihalli

The mean basal area of *T. paniculata* and *L. microcarpa* at the landscape scale was 7.5 m² ha⁻¹ and 4.1 m² ha⁻¹ (Table 2). In MDF, the basal area occupied by *T. paniculata* (9.8 m² ha⁻¹) and *L. microcarpa* (4.1 m² ha⁻¹) characterizes the presence of a high density of individuals represented by the focal species. Both the

species contributed similar basal area (5.2 m² ha⁻¹ and 4.9 m² ha⁻¹) in SEF. In DDF, they were represented by low basal area (0.9 m² ha⁻¹ and 0.2 m² ha⁻¹; Table 2). The basal area of the species in Shettihalli was distributed in the forest types in the order MDF > SEF > DDF, except for *L. microcarpa*, which scored greater basal area in SEF

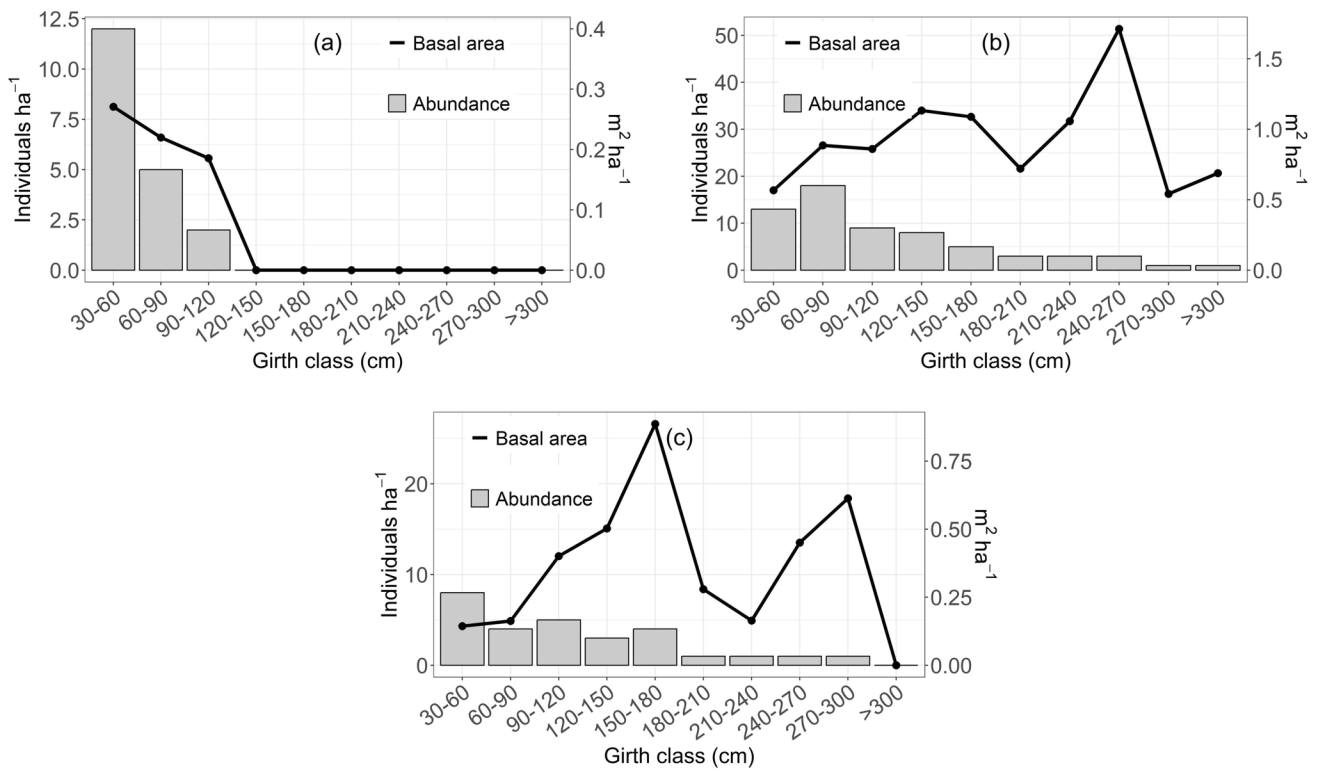


Fig. 4 Population structure of *Terminalia paniculata* in (a) Dry deciduous forest (DDF), (b) Moist deciduous forest (MDF) and (c) Semi-evergreen forests (SEF) of Shettihalli

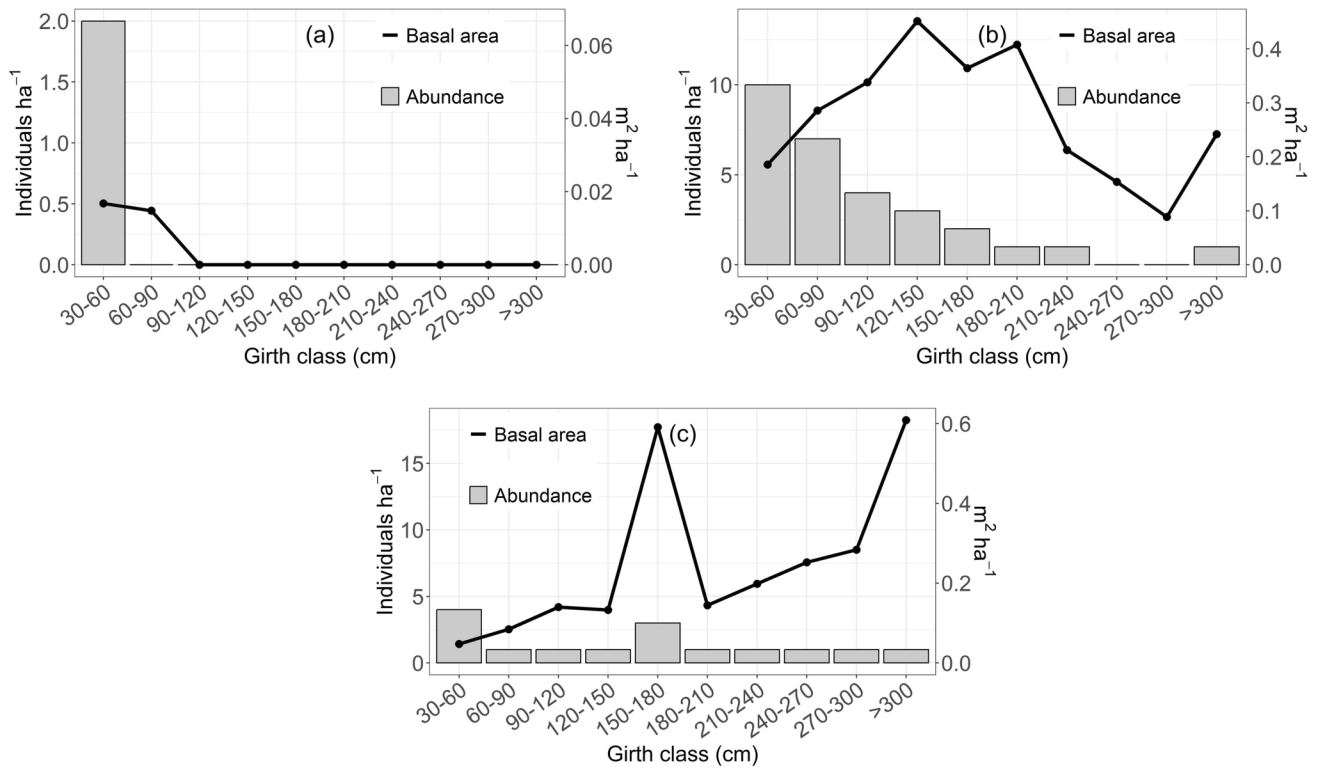


Fig. 5 Population structure of *Lagerstroemia microcarpa* (a) DDF, (b) MDF and (c) SEFs of Shettihalli

compared to the other forest types. Similar to the density, *T. paniculata* displayed a significant variation in the basal area across the forest types ($p < 0.05$; Fig. 3b). Likewise, *L. microcarpa* also showed a statistically significant difference across the forest types (ANOVA; $p < 0.05$), however, no difference was found between MDF and SEF (post hoc; $p = 0.54$; Fig. 3e).

Population structure

The girth class frequency distribution of *T. paniculata* in DDF was characterized by an inverse j-type curve and majorly represented by lower girth classes (30–60, 60–90 cm); with 12 individuals ha^{-1} in the girth class (30–60 cm) and a basal area of $0.27 \text{ m}^2 \text{ ha}^{-1}$ (Fig. 4a). In MDF, *T. paniculata* had 18 individuals ha^{-1} in the girth class (60–90 cm) with a basal area of $0.88 \text{ m}^2 \text{ ha}^{-1}$. As the girth class of the trees increased, the basal area peaked at the higher range (240–270 cm) with an abundance of three individuals (Fig. 4b). In the SEF of Shettihalli, the girth class frequency distribution of *T. paniculata* displayed an asymmetric curve with basal area peaking at two distinct girth classes (150–180, 270–300 cm) with $0.88 \text{ m}^2 \text{ ha}^{-1}$

and $0.61 \text{ m}^2 \text{ ha}^{-1}$ (Fig. 4c). Except for the last girth class ($> 300 \text{ cm}$), the remaining classes had varied individual representations of *T. paniculata*, with the lower and middle girth classes having greater abundance and fewer individuals populating the higher-girth class range.

L. microcarpa in DDF was mainly represented by the lower girth classes (30–60, 60–90 cm) and emulates the partial reverse j-type curve. The abundance of the lower girth class (30–60 cm) was two individuals ha^{-1} with a basal area of $0.02 \text{ m}^2 \text{ ha}^{-1}$. The population structure was similar to *T. paniculata* in DDF, with the absence of *L. microcarpa* individuals in the rest of the girth classes (60–90 to $> 300 \text{ cm}$) (Fig. 5a). The girth class frequency distribution of *L. microcarpa* in MDF showed a reverse j-type curve with the decrease in the abundance from lower girth class to higher-girth classes (Fig. 5b). A gradual increase in basal area was observed with highest contribution by the middle girth classes (120–150, 180–210 cm) with 0.45 and $0.41 \text{ m}^2 \text{ ha}^{-1}$. In SEF, the population pattern represented by *L. microcarpa* was irregular; the basal area peaked in the middle (150–180 cm) and higher-girth class ($> 300 \text{ cm}$). From the lower to middle girth class (30–60 to 150–180 cm), the abundance was more at 30–60 cm, having four individuals

Fig. 6 Heat map showing the species associations (pairwise relationship) determined by the probabilistic co-occurrence model for *Terminalia paniculata* and *Lagerstroemia microcarpa*

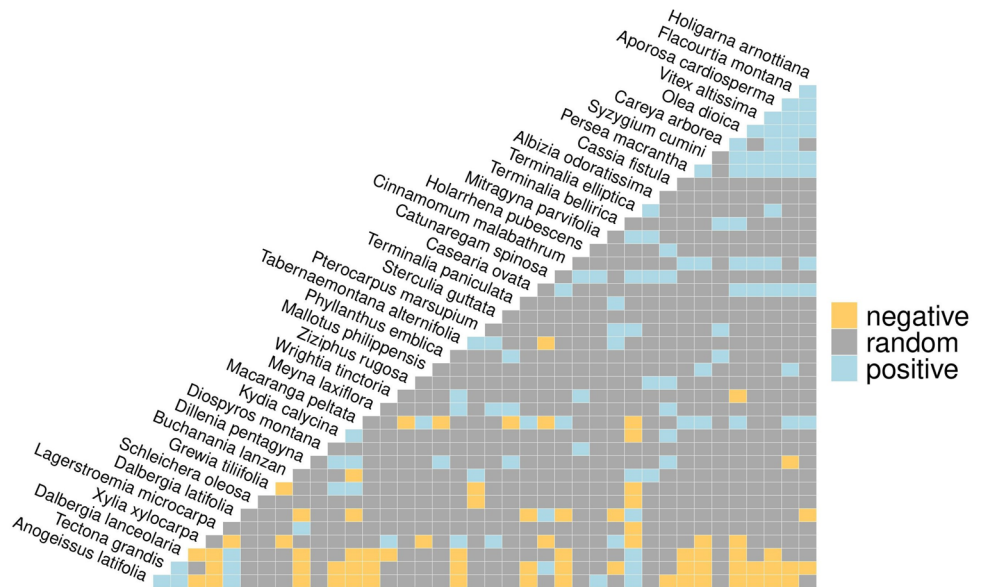


Table 3 Regeneration status of *Terminalia paniculata* and *Lagerstroemia microcarpa* in Shettihalli

Forest type	<i>Terminalia paniculata</i> (Ind. ha^{-1})				<i>Lagerstroemia microcarpa</i> (Ind. ha^{-1})			
	Seedlings	Saplings	Adults	Status	Seedlings	Saplings	Adults	Status
DDF	0	104	27	Poor	0	50	17	Poor
MDF	250	222	86	Good	0	88	42	Poor
SEF	0	105	39	Poor	0	0	37	No
Landscape	250	220	68	Good	0	80	38	Poor

DDF dry deciduous forest, MDF moist deciduous forest, SEF semi-evergreen forest

ha⁻¹. In the following girth classes, the individual representation of *L. microcarpa* tapers until an upsurge at the middle girth class (150–180 cm) with three individuals ha⁻¹. Furthermore, the middle to higher-girth classes (180–210 to > 300) are partitioned uniformly, with just one individual in each (Fig. 5c).

Species associations

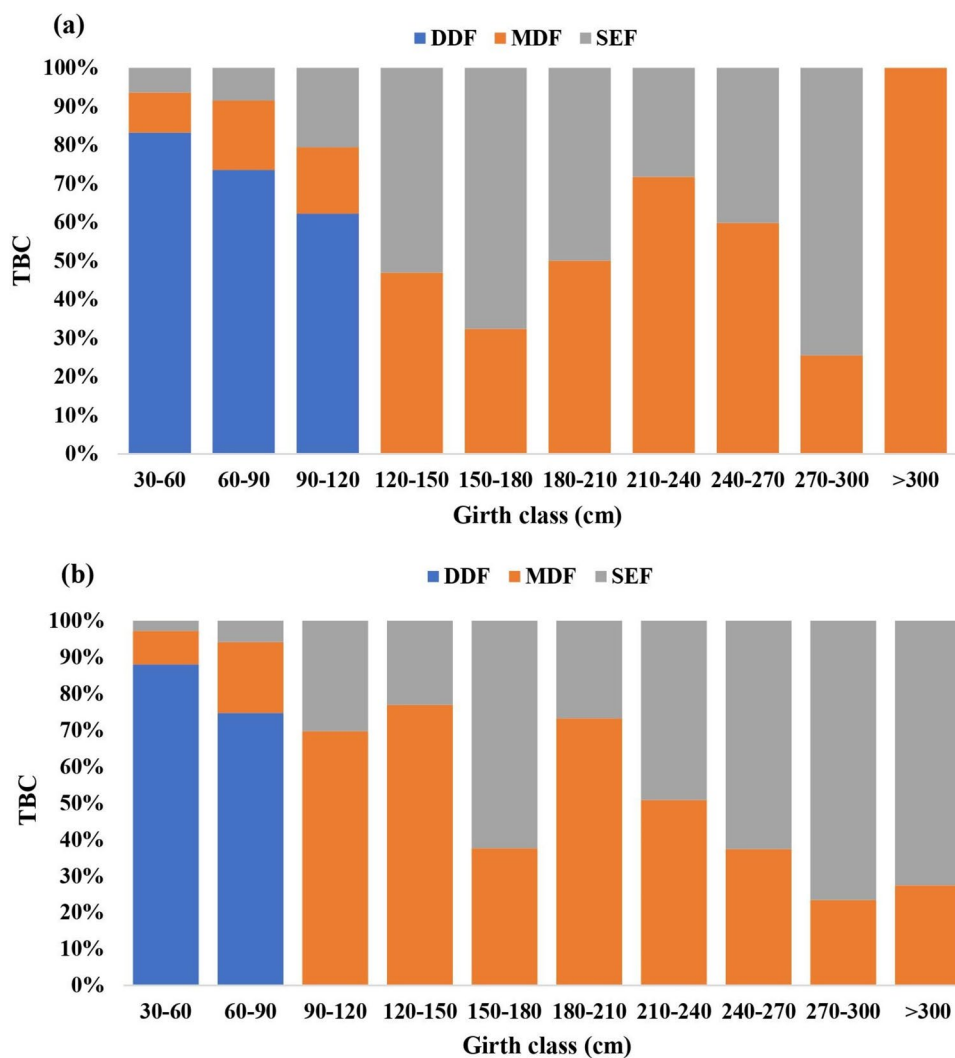
From the one-hundred nineteen, 0.1 ha sample plots surveyed, a total of 39 woody species predominantly occurred in close association with *T. paniculata* and *L. microcarpa* in all the forest types. The tree assemblages (positive, random and negative) emerging in each of them are illustrated in Fig. 6. From the 741 species pair combinations, 0 pairs were removed from the analysis because the expected co-occurrence was < 1. Of the 39 species from 119 plots, 106 formed positive, 73 negative and 562 random co-occurrences. Pair-wise analysis revealed that *T. paniculata* was

positively associated with four species, i.e. *Terminalia bel-lirica*, *Phyllanthus emblica*, *Dillenia pentagyna* and *Meyna laxiflora* and negatively associated with *Macaranga peltata* (Fig. 6). Conversely, *L. microcarpa* was positively associated with *Dillenia pentagyna* alone and negatively associated with *Tectona grandis*, *Anogeissus latifolia*, *Dalbergia lanceolaria* and *Terminalia elliptica*.

Regeneration

The regenerating individuals of the focal species enumerated from subplots were used to estimate density of seedlings, saplings and adults at the hectare scale. Based on the occurrence of *T. paniculata* and *L. microcarpa* in all the forest types, they were categorized into three classes: (1) seedlings, (2) saplings and (3) adults. In DDF and SEF, *T. paniculata* was represented by sapling density–104 and 105 individuals ha⁻¹ and adult density–27 and 39 individuals ha⁻¹, with no seedlings in both the forest types indicating

Fig. 7 Percentage contribution of tree biomass carbon (TBC) based on girth classes (a) *Terminalia paniculata* and (b) *Lagerstroemia microcarpa* in Shettihalli



poor regeneration (Table 3). The recorded seedling densities in the MDF were slightly greater than saplings and adults, thus, signifying an overall good regeneration potential. Coming to *L. microcarpa* in MDF, the saplings and adults were represented by 88 individuals ha⁻¹ and 42 individuals ha⁻¹, respectively, while the seedlings class was devoid of

individuals evincing poor regeneration. Similar results were also obtained for DDF. However, SEF showed ‘No’ regeneration, i.e. no seedlings and saplings, indicating inhibited natural regeneration (Table 3). The regeneration status of *T. paniculata* in the landscape was observed to be good in contrast with *L. microcarpa* having poor regeneration.

Aboveground biomass and tree biomass carbon

For the forest types of Shettihalli, the mean aboveground biomass (AGB) was 69.5 Mg ha⁻¹ for both species (Table 2). The highest AGB recorded for *T. paniculata* was from the MDF at 62.61 ± 6.39 Mg ha⁻¹ and the least from the DDF at 4.71 ± 1.11 Mg ha⁻¹. In the case of *L. microcarpa*, SEF accounts for the majority of AGB at 27.60 ± 11.84 Mg ha⁻¹. The lowest biomass for *L. microcarpa* was from the DDF, at 1.45 ± 0.42 Mg ha⁻¹. The total biomass (TB) and tree biomass carbon (TBC) followed the same trend of AGB by the representation of the highest biomass carbon in MDF followed by SEF and least by DDF for *T. paniculata* and SEF > MDF > DDF for *L. microcarpa*. We found a statistically significant difference in the TBC of *T. paniculata* among the forest types (ANOVA = $p < 0.001$; post hoc = $p < 0.05$; Fig. 3c). Conversely, no significant difference was found in the carbon stocks of *L. microcarpa* across the forest types ($p = 0.22$). But, the post hoc pairwise test revealed a significant difference between DDF vs. MDF and DDF vs. SEF ($p < 0.05$; Fig. 3f). Percentage contribution of TBC across girth classes revealed an asymmetric pattern in

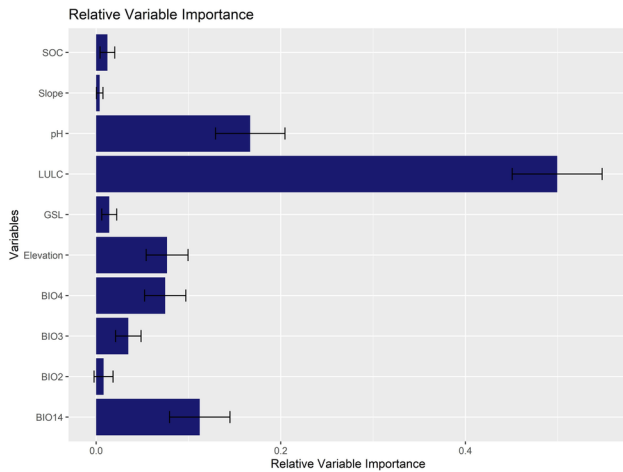
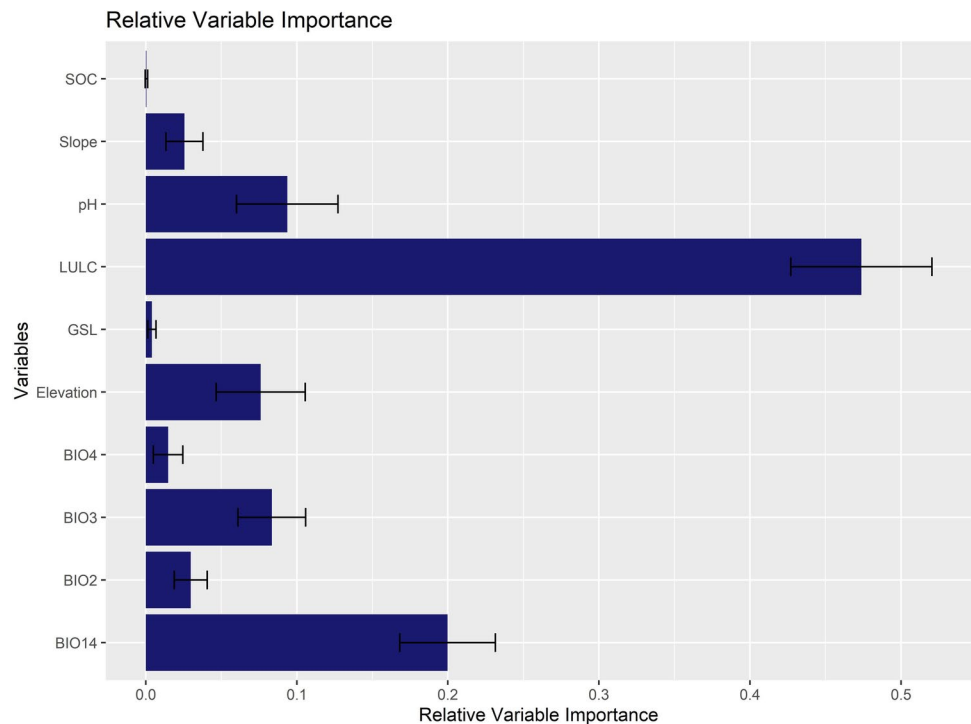


Fig. 8 The relative importance of environmental variables based on the MaxEnt model for *Terminalia paniculata*. SOC soil organic carbon, LULC land use and land cover, GSL growing season length, BIO4 temperature seasonality, BIO3 isothermality, BIO2 annual mean diurnal range, BIO14 precipitation of driest month

Fig. 9 The relative importance of environmental variables based on the MaxEnt model for *Lagerstroemia microcarpa*. Refer to Fig. 8 for variable description



MDF and SEF forests for both the study species (Fig. 7). In DDF, lower girth classes (30–60 and 60–90 cm) contributed more towards the TBC. Comparatively, larger proportion of TBC was recorded in MDF for *T. paniculata* and SEF for *L. microcarpa*.

Multicollinearity, variable importance of environmental predictors and response curves

According to the findings, three (BIO5, BIO7 and Nitrogen) of the 13 variables in this study exceeded the criterion for the evaluation of VIF (> 10); thus, the ten non-collinear variables were used to model the current potential distribution of *T. paniculata* and *L. microcarpa*. (Supplementary Material Table S1). These variables were classified into four major categories viz., habitat (LULC), climatic (BIO2, BIO3, BIO4, BIO14, GSL), topographic (slope, elevation) and edaphic (SOC, pH). The relative contribution of environmental variables varied considerably in their predictive performance based on the MaxEnt algorithm and the order of influence followed habitat (50%) > climatic

(24%) > edaphic (18%) > topography (8%) for *T. paniculata* (Fig. 8). Whereas, for *L. microcarpa*, topography contributed slightly higher than edaphic with an increase in the influence of climatic variables: habitat (47.5%) > climatic (33.5%) > edaphic (9.6%) > topography (10.2%) (Fig. 9).

The variable importance of the MaxEnt model showed that LULC performed the best and was among the top influencing variables, with the most significant contribution of 50% and 47.4% for the habitat suitability of *T. paniculata* and *L. microcarpa*, respectively. Following LULC, pH (16.7 and 9.4%), BIO14 (11.2 and 20%), and elevation (7.7 and 7.6%) were among the other top important variables, with a cumulative contribution rate of 86 and 85% to the modelled potential habitat niche of *T. paniculata* and *L. microcarpa* respectively (Figs. 8 and 9). This suggests that these variables may exert a substantial influence compared to other factors included in this study, therefore playing a pivotal role in determining the distribution of both tree species. Besides BIO14, other climatic variables, BIO4, BIO3 and BIO2, were observed to have a moderate role in determining the distribution pattern of *T. paniculata* and *L. microcarpa*.

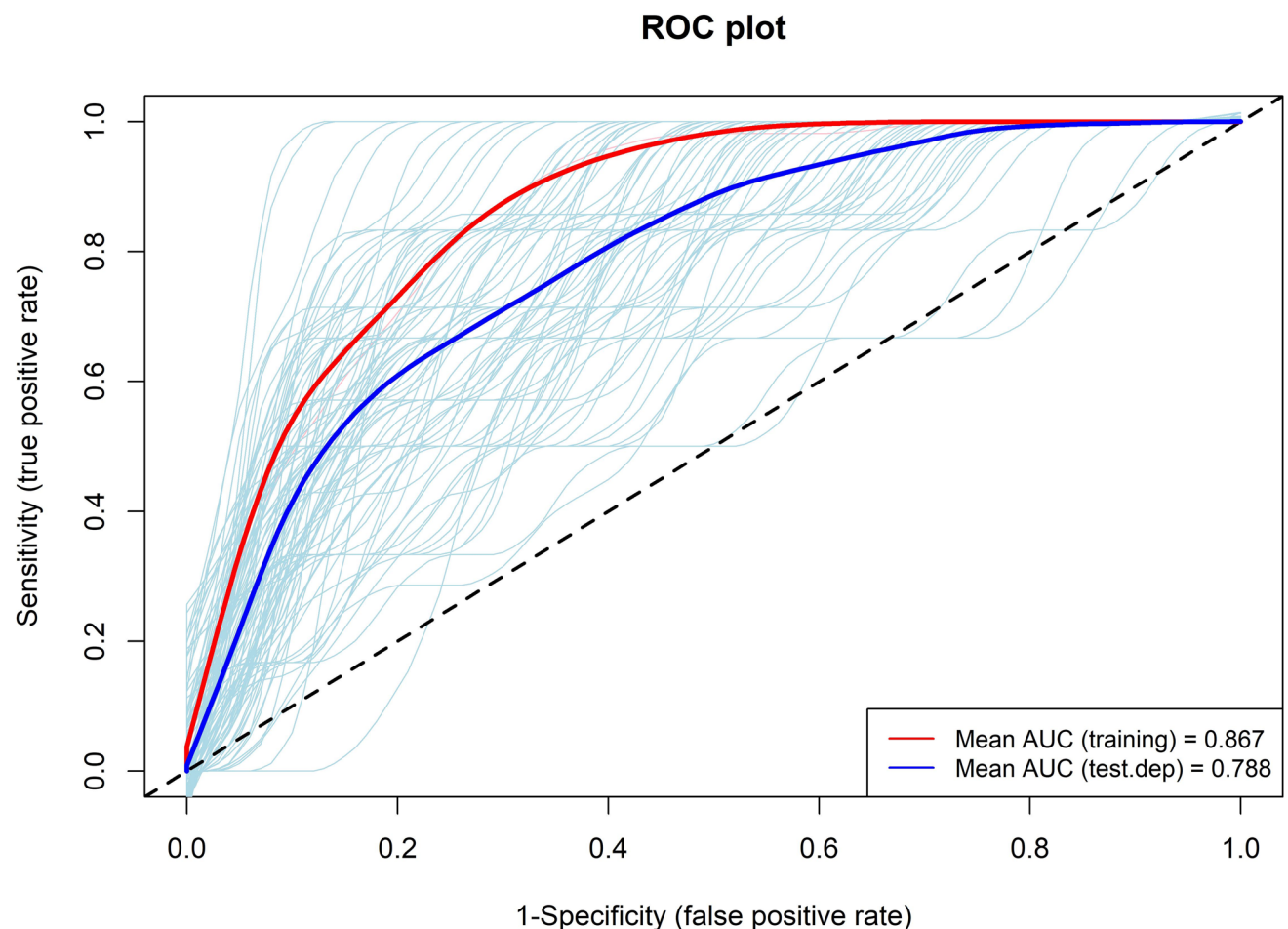


Fig. 10 Receiver Operating Characteristics curve for *Terminalia paniculata*

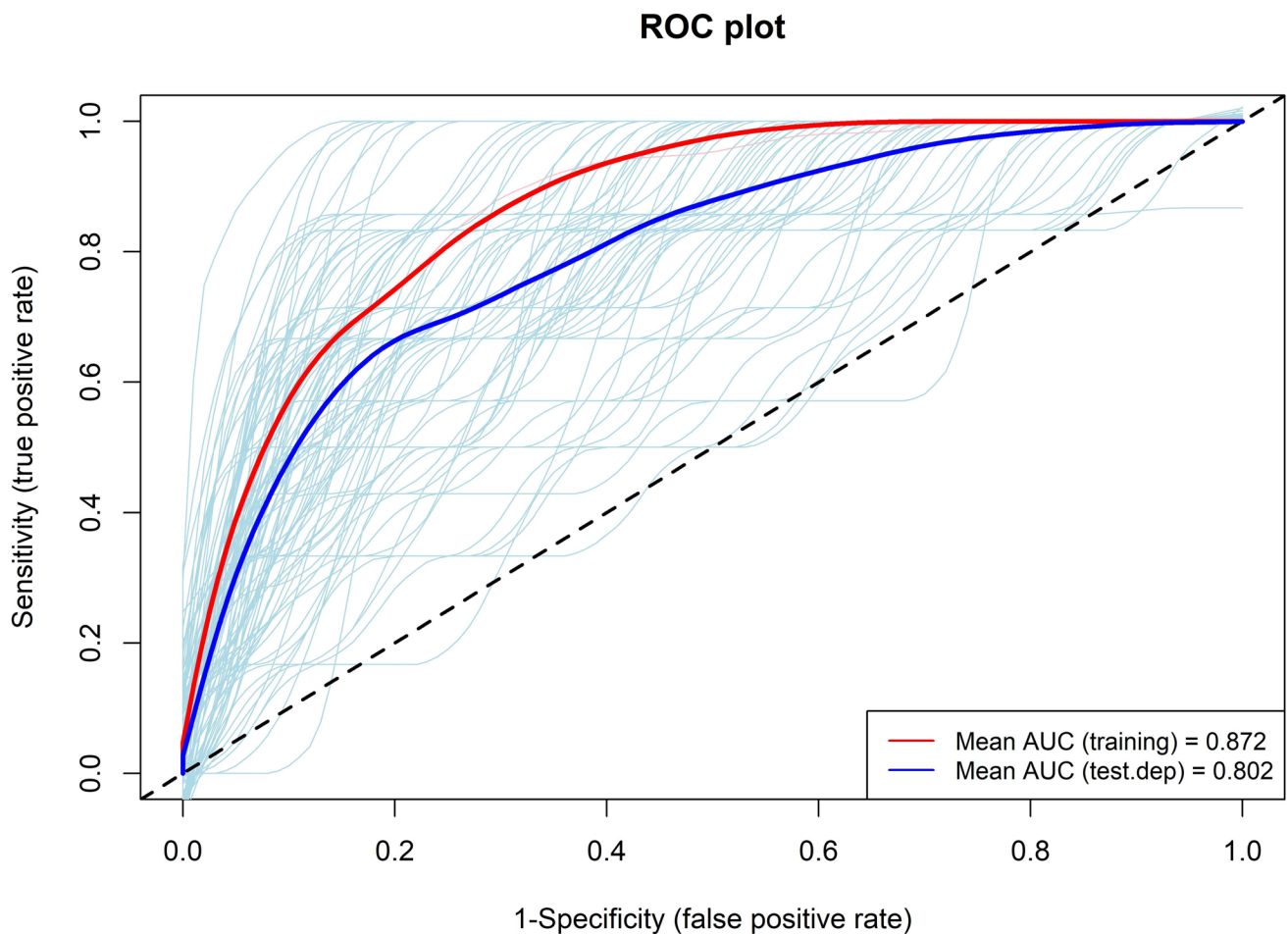


Fig. 11 Receiver Operating Characteristics curve for *Lagerstroemia microcarpa*

Whereas SOC, slope and GSL contributed the least to the model performance, suggesting that they are not highly important in predicting distribution patterns. The most contributing variables are represented in Fig. S1, Supplementary Information.

The response curves elucidated the correlation between the likelihood of species occurrences and the predictor variables, as depicted in Figs. S2 and S3. In the case of *T. paniculata*, the response curves of LULC clearly indicate that natural forests in the Shettihalli had a high probability of species occurrences (MDF > SEF > DDF), followed by settlements and moderate chances near water bodies and in tree plantations. The model found that the likelihood of occurrence of this species was very low in the agricultural and fallow lands (Supplementary Material Figs. S1a and S2). A similar trend was observed for *L. microcarpa* with higher possible occurrences in MDF followed by SEF, DDF and settlement areas (Supplementary Material Fig. S3). Low probability was observed in tree plantations, fallow lands and agricultural fields.

Besides LULC, from the response curves of five other most important environmental factors (Figs. 8 and 9 and Supplementary Material Figs. S2 and S3), it can be inferred that *T. paniculata* is predominantly present in areas where the BIO14 falls within the range of 0.8–1 mm. Additionally, the species is more likely to be found in regions with a pH of six (slightly acidic), elevation below 800 m, BIO4 greater than 1.35 °C and BIO3 range below 0.54 °C. Similarly, the response curves of the key variables demonstrate that the habitat suitability of the *L. microcarpa* is characterized by BIO14 of approximately 1 mm, pH around six, elevation below 600 m and BIO3 below 0.535 °C (see Supplementary Material Fig. S3). Hence, these variables that have been found to offer an estimation of the most important characteristics of the species' habitat suitability and have the potential to influence the distribution of both species in Shettihalli.

Model evaluation

The MaxEnt models of *T. paniculata* and *L. microcarpa* were evaluated by computing the ROC and obtaining the mean

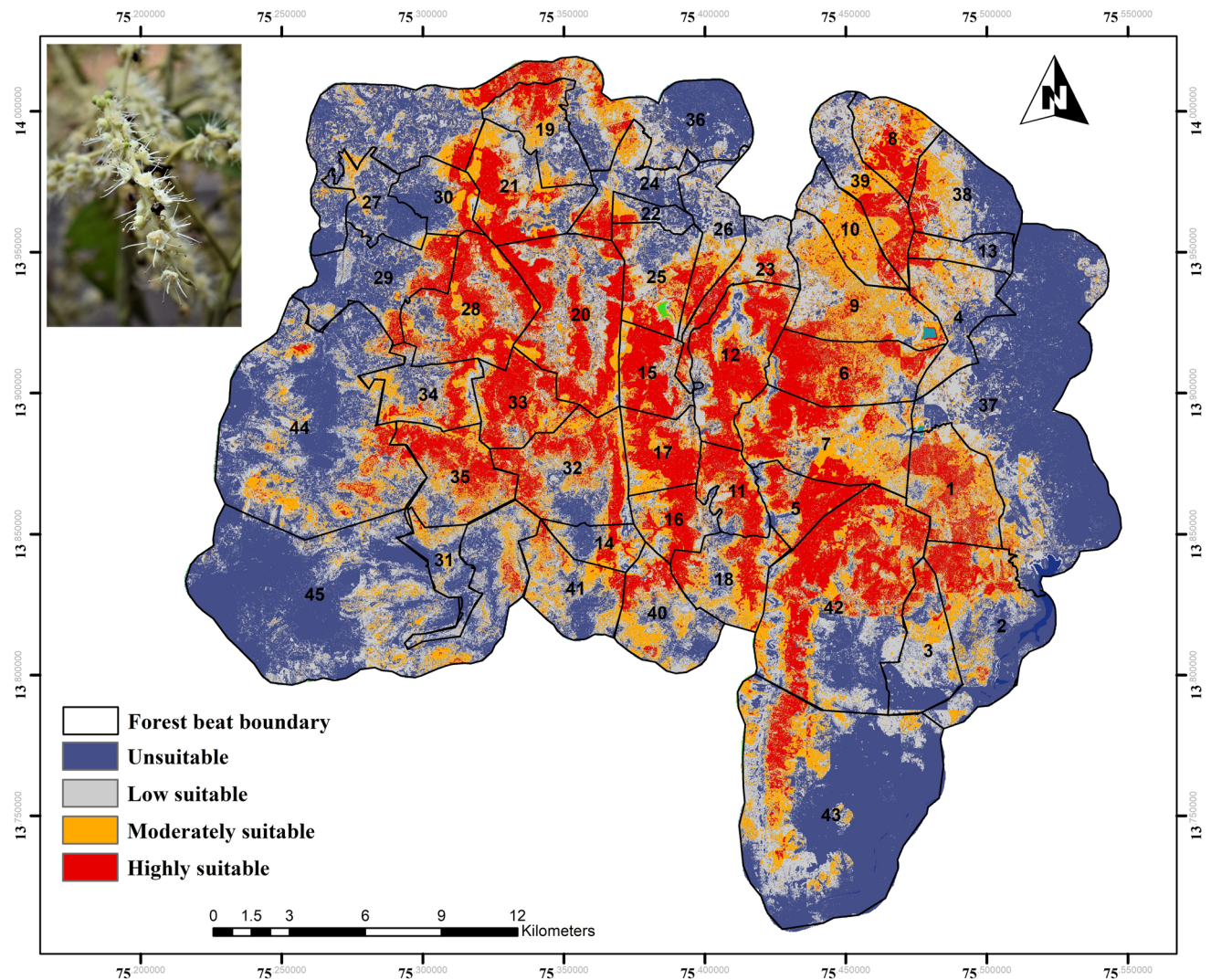


Fig. 12 The current habitat suitability for *Terminalia paniculata* in Shettihalli. Details of forest beats: 1—Sakrebylu north; 2—Sakrebylu south; 3—Thalale; 4—Purudal; 5—Chitrashettihalli; 6—Manjarikoppa; 7—Shettihalli; 8—Anesara; 9—Doddabailu; 10—Ittegehalli; 11—Kalkoppa; 12—Maleshankara; 13—Aldevarahosuru; 14—Alase; 15—Aranelli; 16—Hanagare; 17—Karakurchi; 18—Shiranelli; 19—Basavapura; 20—Belluru; 21—Horohithlu; 22—Adina-

kottige; 23—Sirigere; 24—Chinnakumathi; 25—Kudi; 26—Bilguni; 27—Baruve; 28—Kalasi; 29—Mugudthi; 30—Thammadikoppa; 31—Akalapura; 32—Dobylu; 33—Masakani; 34—Vadahosalli; 35—Vatagaru; 36—Arasalu; 37—Shankar forest; 38—Arekere; 39—Channahalli; 40—Basavanagaddhe; 41—Kombinakai; 42—Mandagadde north; 43—Mandagadde south; 44—Ripponpet north; 45—Ripponpet south

Table 4 Habitat suitability of *Terminalia paniculata* and *Lagerstroemia microcarpa* in Shettihalli

Suitability/species	<i>Terminalia paniculata</i>		<i>Lagerstroemia microcarpa</i>	
	Area (ha)	%	Area (ha)	%
Unsuitable	27,252.13	36.53	35,917.58	48.13
Low suitable	19,541.75	26.19	17,447.23	23.55
Moderately suitable	14,058.26	18.83	9073.18	12.16
Highly suitable	13,765.89	18.45	12,048.68	16.16

AUC to determine its prediction reliability. *T. paniculata* and *L. microcarpa* were represented by $AUC_{T. paniculata} = 0.79$ (Fig. 10) and $AUC_{L. microcarpa} = 0.80$ (Fig. 11), showing satisfactory performance and predictive power for both models. Similarly, the TSS emerged as 0.58 for *T. paniculata* and 0.59 for *L. microcarpa* indicating the model demonstrated fair agreement with the testing dataset. Additionally, the CBI was applied to test the model representing the presence-only data of *T. paniculata* and *L. microcarpa*. Both the models also emerged significantly better than random, as indicated by the Continuous Boyce Index for *T. paniculata*

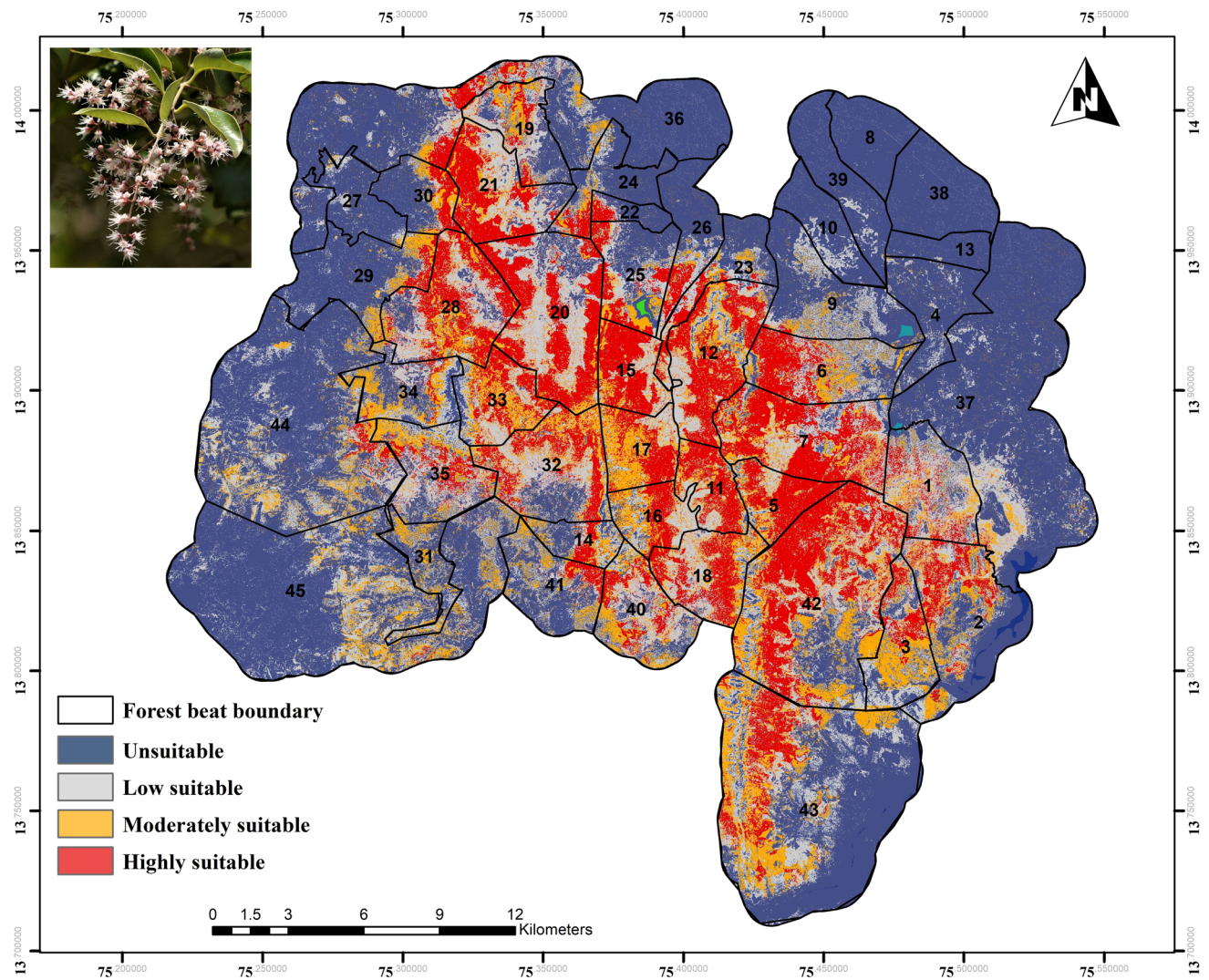


Fig. 13 The current habitat suitability for *Lagerstroemia microcarpa* in Shettihalli. Refer to Fig. 12 for the description of beat numbers

(CBI=0.89) and *L. microcarpa* (CBI=0.95) (Supplementary Material Tables S2 and S3).

Habitat suitability

The generated model showed that 36.53% (272.52 km²) of the landscape is unsuitable for *T. paniculata* (Fig. 12; Table 4). The highly suitable habitat of *T. paniculata* was widespread, covering an area of 18.45% (137.65 km²). Subsequently, *L. microcarpa* is majorly unsuitable, representing 48.13% (359.17 km²) of the Shettihalli landscape (Fig. 13). The highly suitable habitat of *L. microcarpa* represented 16.2% (120.48 km²; Table 4). From the model output, it was observed that highly suitable areas for both species were mainly concentrated on the central to north-western regions of the landscape, mostly preferred lower-middle elevations. We found probable occurrence of both species across the

landscape, particularly *T. paniculata* in the north-eastern regions (moderate and high suitable; Fig. 12) dominated by dry deciduous forests. Whereas *L. microcarpa* showed low to no suitability in the same region (Fig. 13).

Discussion

Stocking density and biomass

As hypothesized, the present study exhibited variation in tree density, basal area and biomass carbon between the forest types for the two studied tree species except for the density of *L. microcarpa*. At the landscape and forest type level, the contribution of both species in terms of density, basal area and biomass are higher than the values reported by Ramesh et al. (2010), who inventoried 96 1-ha plots covering four

different forest types in the entire central Western Ghats. In case of *T. paniculata*, the observed values from the MDF and SEF of Shettihalli are higher than the findings from different tropical forests of the southern Western Ghats (Sundarapandian and Swamy 2000; Magesh 2014; Deepa et al. 2017) and the central Western Ghats (Kulkarni and Hegde 2015). On the other hand, density of *L. microcarpa* is comparable to the northern and central Western Ghats studies (Kanade et al. 2008; Kulkarni and Hegde 2015; Bharathi and Devi Prasad 2017) but lesser than the values reported from southern Western Ghats (Sukumar et al. 1992).

Based on the results, MDFs harboured a higher density of *T. paniculata* and *L. microcarpa*. The number of individuals in MDF could be attributed to the physiognomically deciduous nature of the species, site suitability, soil nutrients and environmental factors such as climate and length of dry season (Ramesh et al. 2010; Toledo et al. 2012; Zhang et al. 2016). Moreover, they are keystone species in characterizing the MDF, as reported in earlier studies (Champion and Seth 1968; Magesh 2014). In contrast to our findings, Krishnamurthy et al. (2009) reported a two-fold higher number of individuals for both the species from Bhadra Tiger Reserve adjacent to Shettihalli. A greater number of *T. paniculata* and *L. microcarpa* individuals were extracted from MDF and DDF of Shettihalli during the colonial period until 1910 due to the high demand for timber (Sarmah 2019), which would have altered the floristic composition and declined the density to a greater extent. The loss of biodiversity in such forest landscapes is frequently caused by the high degree of habitat and population fragmentation, which makes ecologically and economically important species under threat (Jose et al. 2018).

As presented in the current study, tree basal area is a key indicator of growing stock and AGB, where forest types with higher basal areas contributed to higher AGB (Table 2). The reported basal area values are higher when compared to the forests of the Shivamogga region (Hameed 2015) and central Western Ghats (Kanade et al. 2008; Devagiri et al. 2020). A comparison of the aboveground carbon (AGC) of both species from three different forest types in Shettihalli with the average AGC values of tropical forests of India (India State of Forest Report (ISFR) 2021) showed promising results: the AGC contribution by *T. paniculata* and *L. microcarpa* in MDF is 30.7% higher than Indian MDFs. In the case of SEF, the reported values are slightly lesser (12.3%) than the latter. At the same time, a huge difference (85.8% lesser than ISFR 2021) was observed in DDF, which might be due to the poor representation of higher-girth class individuals. The results showed that the MDF and SEFs of Shettihalli are more suitable for conserving these endemic species and sequestering high rate of carbon.

Population structure, regeneration status and influencing factors

As trees contribute to the structural aspects of forests and provide resources and habitat for numerous species, quantifying their population structure and regeneration is another crucial aspect (Iralu et al. 2020; Mohanta et al. 2021). Natural tropical forest systems with good regeneration follow a reverse j-type distribution of population, with the number decreasing from the lower girth classes to the higher-girth classes, signifying a well-balanced density of individuals of the tree species (Paul et al. 2019). Comparing this with the findings of Shettihalli; the landscape has a disturbed population of species fluctuating across the girth classes, with individuals in the girth class (30–60 cm) in all the forest types (with an exception for *L. microcarpa* in MDF) not sufficient to support the stability of future populations. The existence of mature individuals of the species is critical to maintaining a sustainable population in the wild as well as future recovery. However, the number of mature trees (> 120 cm GBH) in Shettihalli is extremely low. As a result, they should be prioritized for conservation to ensure the species' continued recruitment and their subsistence in the community.

The seedling densities of *T. paniculata* are exceptionally low in DDF and SEFs, displaying poor regeneration of this species in the landscape. Though we observed a marginal increase in the number of seedlings in MDF than saplings, they were reported to occur in only 5 out of 72 plots inventoried. The regeneration reported by Pillai and Hrideek (2018) on *T. paniculata* presents a case of poor regeneration attributed to high seed emptiness and anthropogenic pressures. Another potential reason could be the unfavourable climatic conditions during the germination and seedling establishment phases, which might have hindered the regeneration of this species from seeds (Iralu et al. 2020). On the basis of field observations, we hypothesise that the fruits of both species mature in November, which is also the wettest month; thus, the likelihood of seeds getting drained is very high. Though the possibilities for germination are high during February and March, these months are reported to have severe drought, with recurrent forest fires directly influencing regeneration through burning of seeds and seedlings (Sundarapandian and Swamy 2000; Babu et al. 2023b). The same was the case with *Terminalia elliptica*, where authors reported low regenerative capacity as a result of the increased dry period (Mohanta et al. 2021). Regeneration in *L. microcarpa* was represented by no seedlings in any forest type in Shettihalli. This is the case with saplings in SEF, indicating poor regeneration. Though we found the growth of saplings in DDF and MDF, they were twice that of adults, showing slow or poor regeneration potential. According to Valappil and Swarupandan (1996), the intrinsic constraint

of poor embryo viability in the seeds is the cause of the inadequate establishment of *L. microcarpa* seedlings.

No to poor regeneration of the focal species in all the forest types in accordance with previous studies from southern Western Ghats (Sundarapandian and Swamy 2000; Jayakumar and Nair 2013) is caused by moderate to high disturbances by natural and anthropogenic drivers that synergistically cause a detrimental impact on the density of seedlings and saplings and their recruitment. The specific drivers in Shettihalli responsible for regeneration loss are attributable to low seed production, grazing and browsing by fauna, interspecific competition by invasives (*Chromolaena odorata* and *Lantana camara*), trampling, logging, tree pruning, fuel wood extraction and occasional fires (Babu et al. 2021, 2023b; Supplementary Material Fig. S4). Developing artificial regeneration strategies can prevent the loss of young seedlings of endemic species and their subsequent populations. For instance, Nair et al. (2002) successfully demonstrated the artificial regeneration of *L. microcarpa* by raising seedlings in a nursery and planting them in a natural habitat, which had a survival rate of 52%. As these species have a low rate of natural germination, it is necessary to use an adaptation strategy to compensate for the lack of natural regeneration and restore their population by reintroducing nursery-grown seedlings into predicted suitable habitats (Sarma et al. 2022).

Habitat conservation through niche modelling

SDM, also referred to as HSM at the landscape level, is an effective tool for managing forests and its applications in recent times provided a concrete framework for protecting endemic and endangered species from predictable impacts arising from natural and anthropogenic disturbances (Qazi et al. 2022; Rather et al. 2022). The comparison of three performance metrics (AUC, TSS, CBI) revealed that the chosen MaxEnt model is highly consistent and produced good results on par with the studies from the Western Ghats and other tropical forests of the world (Kailash et al. 2022; Agwu et al. 2020; Manzoor et al. 2020; Namitha et al. 2022). Numerous SDMs have been tested to predict the possible distribution of species, but each has its own advantages and disadvantages, including varying degrees of ability to predict the potential distribution of rare, endemic, endangered and medicinally important species (Williams et al. 2009; Mohammady et al. 2021; Meyer et al. 2022). However, MaxEnt is one of the most popular and frequently used modelling algorithms for explicating HSM models (Phillips et al. 2006). Our answers are similar to the findings from other research groups who reported the best performance of MaxEnt in their studies on HSM of *Myristica dactyloides* (Remya et al. 2015), *Ilex khasiana* (Adhikari et al. 2012), *Gymnocladus assamicus* (Sarma et al. 2022); *Quercus semecarpifolia*

(Singh et al. 2021), *Buchanania cochinchinensis* (Mishra et al. 2021), *Melaleuca cajuputi* (Ab Lah et al. 2021), 13 rare tree species from Amazon (Silva et al. 2017) and 62 socio-economically important tree species from tropical and subtropical Asia (Gaisberger et al. 2022).

The findings of this study demonstrate that LULC, the precipitation of the driest month (BIO14), pH and elevation are the main factors influencing the distribution of both tree species. These results are consistent with other works which demonstrated that LULC (Mishra et al. 2021; Xu et al. 2014), soil (Adhikari et al. 2012; Mohammady et al. 2021; Namitha et al. 2022), topography (Meyer et al. 2022) and climate (Castaño-Santamaría et al. 2019; Mishra et al. 2021; Singh et al. 2021; Sarma et al. 2022) played an important role in explaining species occurrences and support our hypothesis that the combination of environmental factors explains the habitat suitability of both species. The results from habitat suitability maps revealed that the current highly suitable habitat for *T. paniculata* and *L. microcarpa* is 18.5 and 16.2%, respectively. The findings echo similar SDM-based research that showed only a small percentage of highly suitable habitats for the other species (Pouteau et al. 2012; Mishra et al. 2021; Meyer et al. 2022), which warrants immediate management intervention and conservation.

Habitat suitability or unsuitability of the focal species is majorly influenced by eight different LULC classes (top contributor based on variable importance) in Shettihalli. As indicated by the response curves, MDF had a high probability of occurrences, followed by SEF and DDF (Supplementary Material Figs. S1a, S2 and S3). Similar to our observations, various scholars reported the occurrence of these species in deciduous and evergreen forest types (Sundarapandian and Swamy 2000; Krishnamurthy et al. 2009; Ramesh et al. 2010) and are principal species in characterizing the MDF (Champion and Seth 1968; Magesh 2014). Furthermore, the ground validation of MaxEnt-based derived high suitable zones during Jan–March 2022 confirms the high occurrence of *T. paniculata* and *L. microcarpa* and the accurate prediction of their distribution in MDF. Moreover, the high suitability coincides with the quantitative analysis of population ecology wherein we reported maximum density, basal area, and TBC of both the species in MDF, reflecting MDFs as potential restoration areas for the regeneration and conservation of both species. Based on the predicted HSM, most of the DDFs are moderately suitable for *T. paniculata* but unsuitable for the growth of *L. microcarpa* (Figs. 12 and 13), which might be due to variations in vegetation composition and climatic conditions. The other potential reason for the suitability of *T. paniculata* in DDF is the ability of the species to tolerate broad environmental gradients and vegetation types (Krishnamurthy et al. 2009; Ramesh et al. 2010; Pillai and Hrideek 2018). Besides natural forests, the response curves showed that the probability of species occurrences

was moderate in settlement regions. This can be attributed to numerous enclosures (124 hamlets) in and around the forests (see Supplementary Information Fig. S1a), mostly represented by few houses. Moreover, they share similar microclimatic conditions of natural forests; thus, the chances of occurrences are high. Forest managers must consider implementing afforestation activities to protect these species by educating people within forest limits.

Various anthropogenic activities significantly impacted the primary contributor, LULC, in this study, altering species' habitat characteristics. Consequently, based on current observations, the current modelled favourable suitability for each species may be broader than predicted. Regions where species are absent might be climatically suitable, and their absence could be attributed to urban or agricultural development factors. An analysis of LULC change spanning 48 years (1973–2022) revealed a decline in forest cover from 78.9% to 66.13%, while agriculture and settlements increased by 4.7% and 10.6%, respectively (Babu et al. unpublished). These factors induce a population crisis for the studied species, impacting primary production, carbon sequestration, and other supporting ecosystem services. Furthermore, the transformed environmental conditions in the ecosystem hinder seed germination and seedling establishment, especially in areas converted to agriculture and fallow lands. In the past, the predominant habitats, corresponding to low-elevation regions and moist vegetation zones, have undergone significant alterations due to anthropogenic activities, leading to habitat modification through housing development, fires, agriculture and conversions into plantations. This transformation suggests that the species is now confined to MDF and SEF, which deserve protection from human impacts.

The second most important factor was BIO14. The response curves showed an increased probability of species occurrences up to 1 mm, and beyond, a sharp decline was observed, indicating that both species are sensitive to the changes in the precipitation and question their ability to thrive in the specific habitat (Rather et al. 2022). BIO14 is important as insufficient rainfall can hinder germination in the subsequent vernal season, consequently constraining the distribution of this species (Xu et al. 2014). Furthermore, the current investigation identified a reduced seed germination capacity in these species within their natural habitat, potentially compromising their reproductive capability and leading to a decline in habitat suitability. Two other important variables, pH and elevation, displayed a characteristic trend in the probable occurrence of both species in the landscape. The response curves for elevation showed a higher probability of species occurrence in the low-lying areas, which explains their suitability by creating microclimates and unique habitat features that influence species distribution via moderating slope and edaphic features (Nguyen et al.

2015; Ahmed et al. 2022). These areas are generally associated with higher temperatures that influence species growth (Hidalgo et al. 2008; Li et al. 2020). Further, warmer temperatures can expand the range for species adapted to or tolerant of these conditions. On the contrary, at medium-higher elevation ranges, the presence of a steep slope can result in poor soil fertility, hence reducing the overall abundance of plant species (Nguyen et al. 2015). Response curves for pH exhibited a higher probability of species occurrence in the pH range of 5.0–6.0, reflecting their ability to grow in slightly acidic soils (Namitha et al. 2022; Saraf et al. 2023). Furthermore, slightly acidic soils can have different microbial communities that can influence nutrient cycling and decomposition of organic matter (Neina 2019).

The potential distribution of a species is intricately linked to environmental factors that are crucial in driving the biological processes of species growth—a pivotal consideration in modelling (Beaumont et al. 2005). Our investigation revealed that the distribution of *T. paniculata* and *L. microcarpa* was moderately influenced by two temperature-related bioclimatic variables (BIO4: temperature seasonality, BIO3: isothermality) in addition to BIO14. Temperature, specifically, plays a significant role in shaping plant growth and distribution by regulating important physiological and biochemical activities such as photosynthesis, respiration, and material transfer (Walther et al. 2005; Shi et al. 2022). The finding that a higher probability of *T. paniculata* occurrences is associated with increased temperature seasonality, as derived from response curves, suggests a strong ecological correlation. This pattern indicates that the studied species likely exhibit preferences or adaptations to seasonal temperature fluctuations, with temperature acting as a key factor influencing their distribution (Gaikwad et al. 2011). The ecological significance of this association might be due to the diversity in phenological patterns influenced by variations in abiotic conditions across seasons (Raes et al. 2009). Alternatively, it could be attributed to the heightened temporal habitat heterogeneity, leading to increased available niches (Raes et al. 2009; Spiers et al. 2018).

The observation that a higher probability of species occurrences is associated with lower isothermality suggests that *L. microcarpa* in the studied area prefers less variable temperatures across seasons. Isothermality, which represents the uniformity of temperature throughout the year, appears to be a significant factor influencing the distribution (Xu et al. 2014; Fan et al. 2022). Several potential explanations for this inverse relationship include: First, species adapted to more stable temperature regimes may find the conditions under lower isothermality to be more favourable for their life history traits, reproductive strategies, or resource utilization. Second, reduced temperature variability might contribute to habitat predictability, supporting the persistence of populations over time. Third, species may have evolved specific

adaptations to cope with or take advantage of the relatively constant temperature conditions associated with lower isothermality (Fan et al. 2022).

Recent research by Gardner et al. (2019) supports using physiologically relevant climate variables related to the growing season, soil water content, temperature, and annual and summer precipitation. These variables, closely tied to the biological processes of the study species, provide more accurate representations of the climatic requirements influencing their distributions (Kearney and Porter 2009). As a direct link between climate and physiology, proximal variables associated with inherent physiological limits are likely to consistently influence a species' distribution across time and space (Austin 2002). Among the three physiological variables considered in this study, we found high collinearity between the two physiological variables, growing season temperature (GST), growing season precipitation (GSP) and some bioclimatic variables during the multicollinearity test; thus, they were omitted from further analysis. Further, these correlations can pose challenges in selecting bioclimatic variables for modelling. Therefore, there is a need for more focused studies elucidating the significance of physiological, climatic, edaphic, and topographical factors in determining the habitat of plant species and in modelling future climate scenarios. On the other hand, the role of growing season length (GSL) was very poor, and the significance of other variables in the optimal model indicates that it may not play a prominent role in predicting distribution patterns. This study did not incorporate additional physiological variables due to data unavailability, as constructing these variables requires data which are presently lacking (Kearney and Porter 2009). Unlike bioclim variables, which are readily accessible at 1 km resolution, no comparable dataset exists for physiological variables (Gardner et al. 2019).

Climate change is anticipated to induce global shifts in species distributions, jeopardizing their survival through range reductions and impacting their representation in protected areas. Biodiversity hotspots, hosting numerous species with small ranges, are particularly at risk as they may contract further while species seek their optimal habitats (Velásquez-Tibatá et al. 2013). Predictions from multiple climate models indicate a future rise in temperature and precipitation across all seasons in India. By the end of the century, temperatures are expected to increase steadily, with a maximum warming of 4–5 °C, and precipitation is projected to rise by $\sim 2 \text{ mm day}^{-1}$ or 15–24% (Bal et al. 2016; Salunke et al. 2023). Hence, it can be deduced that climate change exerts profound effects on species ecology, physiology, phenology, regeneration and distribution, influencing population sizes and altering geographical ranges (Miller-Rushing et al. 2010; see Shi et al. 2022 and references therein; Hazarika et al. 2023). The predicted extreme precipitation induces water saturation, impacting nutrient availability (Stan and

Sanchez-Azofeifa 2019). Secondly, high precipitation leads to soil erosion and poor fertility, restricting the growth of woody species (Bedane et al. 2023). At the same time, the temperature rise may prompt a shift to higher elevations, while elevated CO₂ affects water use efficiency and drought sensitivity (Song et al. 2004; Shi et al. 2022). Research indicates that plants exhibit heightened sensitivity to alterations in soil properties caused by temperature fluctuations (Sullivan et al. 2015). The combined effect of these changes leads to the fragmentation of suitable habitats and a decline in habitat quality, posing a threat to species persistence. This is particularly detrimental for endemics with small ranges; reductions in range size pose higher risks (Spiers et al. 2018).

The projected increasing trend in precipitation and temperature over our study area and their associated impacts may likely intensify the susceptibility of both species to ongoing climate change. Therefore, understanding changes in suitable distribution areas is crucial in future climate change scenarios and implementing targeted conservation measures is essential for enhancing the effectiveness of biodiversity conservation (Remya et al. 2015; Shi et al. 2022; Hazarika et al. 2023). However, this study refrained from modelling future projections of species distribution in a climate change scenario due to the predominant influence of LULC on the current distribution and the absence of data on LULC change. Moreover, it is inappropriate to assume habitat constancy, particularly given the anticipated changes resulting from climate change and land use modifications (Ferretto et al. 2023). Consequently, excluding LULC becomes critical when a species displays strong habitat fidelity, as substantial changes in the modelled distribution can occur with significant shifts in habitat (Ferretto et al. 2023).

Implications for conservation and restoration

A disturbed landscape is a characteristic feature of secondary MDFs (Chokkalingam and De Jong 2001). The species *T. paniculata* and *L. microcarpa* belong majorly in such a forest type in Shettihalli. Currently, Shettihalli is under threat due to disturbances from villages surrounding in the sanctuary, the perturbations recorded include logging, collection of fuel wood and twigs, forest fires, trampling of seedlings, agriculture, encroachment, and seasonal collection of fuel wood. Typically, the major direct driver responsible for diminishing the populations of the focal species is illegal logging, for use as fuel wood and fencing posts. As a result, tree stumps of the lower and middle girth classes were encountered in the landscape, which influence the stand dynamics by exhibiting recruitment loss of new, mature individuals intended to augment the extant populations (Käber et al. 2021). In addition, leaves and branches of trees and

understory vegetation are conventionally utilized as bedding material for cattle sheds (Nayak et al. 2000). These species will continue to decline from their native habitats soon if unsustainable operations are not curtailed and compensated with restoration activities in suitable habitats. From a socio-economic viewpoint, many local people are not completely aware of the economic and ecological importance of both the species. Such knowledge demands widespread awareness among the people.

The poor regeneration potential of the species with low seed germination reported by other researchers might lead to population decline and habitat suitability. Two invasive alien species, *L. camara* and *C. odorata* dominated the Shettihalli landscape (Babu et al. 2021, 2023a) and frequently co-occurred with the two endemic trees species and other native flora. As a result, local biodiversity is threatened by the allelopathic effect of these invasives (Sundaram and Hiremath 2012). Conservation measures are necessary to curtail ongoing biodiversity loss due to invasion. This is not the case with just two species alone; in a recent study Gaisberger et al. (2022) pointed out 63 tree species of socioeconomic importance from 20 different countries are threatened due to over-exploitation, habitat destruction, fire regimes, excessive grazing and climate change affecting their natural distribution. This demonstrates the necessity of intensifying focused conservation and restoration actions for native diversity of tropical and subtropical Asia for preventing valuable tree species from local extinction.

Given that trees with large size classes (10 cm DBH) frequently make the highest contribution to AGB (Djuikou et al. 2010) and have a significant impact on the AGB storage across various tropical forest (Silva Costa et al. 2012). In our investigation, the majority of AGB was in trees with a larger diameter. Their elimination significantly changes the dynamics of the biomass in this area and substantially affects species richness and composition (Suratman 2012). Restoration initiatives are effective for improving species composition and regeneration, reducing carbon emissions and enhancing carbon sequestration through human-induced local forest restoration in sensitive ecosystems, such as the Western Ghats. For instance, in an Atlantic Forest, the AGC increased by approximately 20% after three decades of natural regeneration, with a recovery of 65% and 30% of the region's threatened and endemic species (Matos et al. 2020).

It is impossible to effectively conserve endemic species in the biodiversity hotspots without involving other plant species in restoration programs that share the same ecological niche (Rather et al. 2022). Our plot inventories, however, showed that the plant communities with many tree populations of *T. paniculata* and *L. microcarpa* are mainly comprised of four species (*T. bellirica*, *P. emblica*, *M. laxiflora* and *D. pentagyna*) and are found only in the MDF of Shettihalli. As a result, the existence of this species pool and

MDF may serve as a potential indicator of suitable sites for restoration (Gaisberger et al. 2022). Shettihalli has a vast land area set aside for conservation reserves, besides considerable portion of degraded forest patches that can be utilized for restoration programs. Hence, activities like afforestation, reforestation and restoration through natural regeneration offer a huge potential under Reducing Emissions from Deforestation and Degradation (REDD+). Research revealed that species like *T. paniculata*, *Dalbergia latifolia*, and *L. microcarpa* are able to recover and establish in the interspaces between the *Eucalyptus* and teak plantations (Hameed 2015; Babu et al. 2023a). Shettihalli holds about 10,000 ha of mono-and mixed teak, *Acacia*, *Pinus* and *Eucalyptus* plantations in the landscape (Babu et al. 2023a) which can be considered for regeneration and sustenance of these endemic species.

The studied species are endemic to the Western Ghats and peninsular regions and possess a range of ecological functions and services (Nair et al. 2002; Pillai and Hrideek 2018). A comprehensive understanding of the species distribution is essential for the successful restoration and sustainable utilization of these species. According to our findings, the habitat specificity of both species may lead to a rapid fall in its stability and sustainability if timely conservation measures are not implemented. The cumulative effects of ongoing human activities and climate change can result in significant degradation of the natural habitats of these species. The habitat suitability maps of *T. paniculata* and *L. microcarpa* in Shettihalli exhibited 1/3rd and 1/4th of moderate to highly suitable areas composed of four major LULC classes, i.e. MDF, SEF, DDF and tree plantations. The major hotspots for *T. paniculata* were found in Sakrebylu north, Anesara, Channahalli (dominated by DDF, MDF and teak/*Eucalyptus* plantations); Chitrashettihalli, Manjerikoppa, Kalkoppa, Maleshankara (MDF, SEF and teak plantations); Aranelli, Karakurchi, Kalasi, Maskani, Hanagare (MDF; SEF), and Mandagadde north (SEF and MDF (Fig. 12; Supplementary Information Fig. S1a).

On the other hand, the important regions of conservation prioritization for *L. microcarpa* include Sakrebylu south, Thalale, Chitrashettihalli, Shettihalli (composed of MDF and teak plantations); Kalkoppa, Maleshankara, Aranelli, Karakurchi (MDF, SEF and teak plantations); Hanagare, Belluru, Horohithlu, Kalasi, Maskani (MDF and SEF); Mandagadde north and south (MDF and SEF) regions (Fig. 13; Supplementary Information Fig. S1a). The observed suitability of these vegetation types is further supported by the results obtained in the study, actual field observations and the findings of Babu et al. (2023a); therefore, these regions can serve as potential habitats for effective conservation and restoration. By doing so, the habitat suitability for both species can be enhanced, thereby benefiting not only this species but also various other endemic species that play a

crucial role in maintaining the ecosystem functioning within the study area. Furthermore, future populations of *T. paniculata* in DDF and SEF and *L. microcarpa* in the entire landscape may be under threat as a consequence of poor regeneration; in this scenario, the predicted habitats of high suitability can be transformed as restoration sites for in-situ conservation (Yang et al. 2013). Endemic tree species are more likely to become extinct due to their susceptibility to natural disasters and anthropogenic pressures (Coelho et al. 2020) in many areas, including the Western Ghats (Chitale et al. 2014). To conserve species from current and future threats of extinction, MaxEnt becomes an invaluable tool to monitor the present and future status of species. Overall, the findings support the hypothesis that the integration of ecological attributes, habitat suitability-dependent factors and the MaxEnt model's accuracy can be a valuable tool for determining the appropriate habitat of the studied tree species for conservation and successful restoration in the most suitable areas.

Conclusion

The population assessment in the ecologically sensitive zone of the (central) Western Ghats biodiversity hotspot explored community ecology attributes that led to significant insights into the ecological status and potential distribution of the two endemic species. The uneven population structure of the focal species in almost all the forest types signifies vulnerability in future sustenance of the individuals in the represented girth classes. Such discernible irregularities in populations arising from various causal factors increase tree mortality, thereby lessening the addition of large-girth individuals into the existing population regime. Our study revealed that the studied species provide a key regulating service by stocking high levels of carbon. The carbon storage from all the girth classes is prominently predicated upon the species' dominance and high basal area. Hence, it is important to conserve and maintain extant large-girth individuals that aid in the sustained regeneration of the species and provide innumerable ecosystem services. The poor regeneration and diminishing population structure in the Shettihalli landscape highlight the detrimental effects of excessive grazing, trampling, invasive species, forest fires and the rigorous debranching activities carried out by the local people that prevented the successful establishment of seedlings. Therefore, it is necessary to introduce awareness-raising and monitoring programs to improve the existing condition and reinstate the existing forested and degraded areas. Our approach enabled identification of most suitable areas in the landscape for restoration activities. Based on the habitat suitability modelling, MDFs are highly suitable for growth, regeneration, and re-introduction of both species,

followed by SEF. Prioritizing critical areas of high suitability in conjunction with appropriate conservation measures in Shettihalli landscape provides necessary directions and inputs for effective management and restoration of species. It is recommended that in-situ conservation be carried out with the help of local communities, forest department, and frequent population monitoring and through development of conventional propagation techniques. The findings of our study have consequences for the preservation of endemic flora in biodiversity hotspots, considering the urgency with which we must identify regions that need to be conserved. To persuade more actions in conservation and assist endemic and threatened plants in gaining attention, this work encourages further investigation into the possibility of including ecological inventories with the integration of user-friendly SDM modelling techniques in similar underexplored biodiversity-rich forests. Finally, the data generated from this research will be an asset for future regional-level IUCN Red List assessments.

Author contribution statement KNB: Conceptualization, Methodology, Software, Field work, Formal analysis, Validation, Writing—Original draft preparation; SJ: Field work, Writing—Original draft preparation; KA: Field work, Writing—Reviewing and Editing; RG: Software, Formal analysis, Validation, Writing—Reviewing and Editing; SM: Field work, Writing—Reviewing and Editing; NA: Conceptualization, Project administration, Funding acquisition, Supervision, Writing—Reviewing and Editing; NA: Supervision, Writing—Reviewing and Editing. All authors read and approved the final version of the manuscript.

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Data availability Species occurrence coordinates can be obtained on a reasonable request from the corresponding author. Due to privacy concerns and MoU between the parties, the data are not publicly accessible since they are being used to create other reports for funders.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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