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Analysing highly biodiverse tropical dry forests for improved conservation

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Abstract

Tropical dry forests (TDF) support the livelihoods of millions of people worldwide, but in contrast with the humid tropical forests, knowledge of their structure and biology is limited. This study aims to fll that gap using observations from the South Indian Deccan Plateau. Based on large, tree-mapped feld plots, within or near a densely populated metropolitan area, we present details of 130 woody plant species, including a large number of climbers. The modelling approach includes a new function for developing species–area relations (SAR's). In addition to the greater fexibility of the function, when compared with traditional power and asymptotic functions, the *Monod* function not only provides greater fexibility, but also allows reasonable estimates of SAR's if the overall regional species richness is known. This is an important advantage when compared to the standard methods. Another new fnding concerns the species abundance distribution (SAD) which explains processes of community assembly and species turnover. The SAD follows the Weibull model which is a signifcant improvement compared with the traditional use of the Lognormal model because the Weibull parameters seem to be related to species richness. We also present a new cell-based (in addition to the individual neighbourhood-based) approach for analysing structure. The cell-based analysis combines small-grain measures of density and crowding, richness and size variation and can be used to assess the degree of similarity or dissimilarity among forest stands, or between a current and some ideal target structure. The methods of analysis and the proposed framework for pro-active conservation presented in this study may be helpful in regions of the world where complex multi-species forests require advanced methods for sustaining their resilience and functions.

Keywords Tropical dry forest · Individual structure · Cell-based structure · Forest biodiversity · Long-term observational studies

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Introduction

Tropical dry forests (TDFs) are found between 10° and 25° latitude, usually north and south of the world's tropical rainforests. The most extensive areas of tropical dry forest are found in South America, sub-Saharan Africa and India. Significant concentrations are also present throughout Southeast Asia, northern Australia and parts of the Pacifc, Central America and the Caribbean (Blackie et al. [2014a,](#page-14-0) [b](#page-14-1)). With a dry season that lasts six or more months of the year, the climate is signifcantly more seasonal than that of a rainforest. Dry forests comprise slightly less than half of the world's subtropical and tropical forests and support some of the world's poorest people. For example, the African Miombo woodland alone is thought to provide livelihoods for more than 100 million people in urban and rural areas (Dewees et al. [2011\)](#page-14-2). As a result, tropical dry forests around the world have been extensively devastated by deforestation for agriculture and human development. TDFs harbour numerous woody plants, including a great variety of climbers. Climbers are plants that are rooted in the ground using other plants for support. The climbers that were identifed in the three permanent study areas were classifed based on the mode of climbing as twiners, lianas and stragglers. Lianas are long-stemmed woody plants that use the support of a tree eventually growing up to the canopy in search of sunlight. Twiners (or stem climbers) are "twining" themselves spirally around a supporting tree. They may reach the canopy, but are mostly restricted to the understorey. Stragglers (ramblers) are plants that do not climb but somehow manage to support themselves by clinging to the trunks, stems or branches of other plants. Stragglers have specialized organs, such as prickles, spines or thorns that are used for support.

Despite their importance, tropical dry forests are among the most threatened and least studied of the world's forest ecosystems and, as a result, are at even greater risk of disappearing than humid forests, primarily due to higher population densities and the associated demand for energy and land (Blackie et al. [2014a,](#page-14-0) [b\)](#page-14-1). Much of the data required for policy are absent or incomplete. Site-specifc data are urgently required for evidencebased policy and management decisions (Blackie et al. [2014a,](#page-14-0) [b\)](#page-14-1). The minimal attention paid to dry forests led Meister et al. [\(2012](#page-15-0)) to state that "almost nothing is known about tropical dry forests". Such statements provide sufficient incentive for research. The tropical dry deciduous forests of the South Indian Deccan Plateau are represented by a few protected remnants of very particular ecosystems within densely populated areas. These protected remnants provide the basis for our study.

Based on a new research infrastructure and advanced analytical tools, it is possible to improve our understanding of the biology, structure and dynamics of these complex ecosystems and thus provide essential information for management and conservation. Particular objectives of this study are: 1. to apply advanced methods of structural analysis of the three study areas; 2. to assess biological diferences among the three study areas based on species–area relationships and species abundance distributions; 3. to propose a framework for pro-active conservation to ensure the sustainable functioning of these unique ecosystems. We expect that our study will contribute to improved understanding of these communities, promote greater awareness of dry tropical forests among scientists and thus contribute to more efective conservation.

Methods

Study areas

Three large protected feld permanent preservation plots (PPPs) of 1 hectare each (100 m \times 100 m) were established as per the Centre for Tropical Forest Science protocol (Condit [1998\)](#page-14-3). The plots are designated Bugarikallu (Bg), Thalewoodhouse (Tw) and Doresanipalya (Do). The detailed description of the methods followed for plot establishment, enumeration and spatial analysis is described in Kakkar et al. [\(2018](#page-14-4)). GPS coordinates and elevations are presented in Table [1.](#page-2-0) The three study areas, shown in Fig. [1](#page-2-1) in relation to their immediate surroundings, enjoy a high degree of protection. Heavy rainfall occurs during the months of September and October from the North-east monsoon and torrential rains from June to August from the South-west monsoon. Annual rainfall (based on South-West monsoon, North-East monsoon and Pre-monsoon) varies between 417 and 1494 mm with a mean of 869 mm measured during the period 1960–2016; occasionally the area receives heavy cyclonic rains in October and November. The mean annual temperature is around 24.7 \degree C with a maximum 39.4 \degree C and a minimum of 10.2 °C. The soils have been classifed as silty clay loam (Thalewoodhouse), sandy clay (Bugarikallu) and loamy sand/ sandy loam (Doresanipalya). Detailed descriptions are presented by Raju ([2014\)](#page-15-1). The Doresanipalya plot is surrounded by urban settlement with a high population density in the suburbs of the city of Bengaluru. Thalewoodhouse and Bugarikallu are located in the Bannerghatta National Park which is shown in green colour in Fig. [1.](#page-2-1) All three sites are strictly protected and located in close vicinity to each other (distances are shown in Table [1](#page-2-0)).

Details of woody species

The details of each woody plant species will be presented, separately for each plot, including plant taxonomies, taxonomic ratios and number of introduced or invasive species. A brief summary of the 22 species of climbers encountered in the three study areas is also presented. The climbers are classifed based on the mode of climbing as *twiners*, *lianas* and *stragglers*.

Quantitative methods

The literature about forest structure is extensive, even an incomplete review would require much space which would dilute the focus of this contribution. The interested reader is referred to the studies of Pretzsch [\(1993](#page-15-2), [1997\)](#page-15-3), to two new approaches for natural forests (Lujan-Soto et al. [2015;](#page-14-5) Keda et al. [2022](#page-14-6)) and to the comprehensive review of Pommerening and Grabarnik [\(2019](#page-15-4)) on forest structure. The emphasis on the biological characteristics of forest structure, in contrast with the traditional physical attributes of structure, is still rarely found in the journals of forest science. It is believed that this will become increasingly important, in view of climate change efects on forest resilience and functioning. For this reason, particular attention is given to our new methods of developing species–area relationships (SAR's) and species abundance distributions (SAD's), and to the assessment of diferences between forests, or between a current condition and some target state that may be efective in sustaining resilience and functioning.

Table 1 GPS coordinates and elevations of the four corner points (1, 2, 3, 4) of the Bugarikallu (Bg), Thalewoodhouse (Tw) and Doresanipalya (Do) plots

The distances are shown in the table at right with Thalewoodhouse as central point (6.03 km between Bg1 and Tw1); (14.55 km between Tw1 and Do1)

Fig. 1 Location of the three study sites to the south of the Bengaluru city centre. The three study sites and their immediate surroundings *are shown in diferent colours*

The species–area relationship

To allow comparisons of the study sites in terms of species richness, it is necessary to develop a relation between the contiguous plot area and the number of species in each plot. A number of models have been proposed to describe the species–area relation (de Caprariis et al. [1976](#page-14-7); Gitay et al. [1991](#page-14-8); Monod [1950](#page-15-5); Tjørve [2003](#page-15-6); Williams [1995](#page-15-7)). Asymptotic functions are appropriate in very large plots where all species are likely to be captured by the samples. The power function is more suitable for small plot sizes where the maximum number of species is unknown. The hitherto almost unknown *Monod* function (Monod [1950\)](#page-15-5), which represents a fexible compromise that includes the advantages of both, the power function and the asymptotic functions, will be used in our study to estimate the species–area relation:

$$
S = \frac{a \cdot A}{1 + b \cdot A} \tag{1}
$$

where *a*, *b* are empirical parameters; *S* is number of species; *A* is a contiguous forest area (m^2) . We derive such a species–area relation by assigning sample plots of increasing size to random positions within the study area. The sampled area and associated number of species are used to derive a species–area relation (SAR) for the whole study area. Equa-tion [\(1](#page-3-0)) has the following properties: (1) when $A=0$, then *S*=0; (2) *S* increases with increasing *A*, until an asymptotic value (S_{max}) is reached; (3) the estimated maximum number of tree species equals *a/b*, which is useful for comparisons among diferent communities.

The species abundance distribution

The species abundance distribution describes the abundances of all species recorded within a forest community of interest. The SAD may explain processes of community assembly and is believed to be one of the most ubiquitous patterns in ecology (Matthews and Whittaker [2014](#page-14-9)). We estimate the SAD using the Weibull distribution:

$$
LN = k \cdot e^{(-SR/b)^c}
$$
 (2)

where LN is the estimated logarithm of the number of individuals; *k* is the log (number of individuals of species 1, i.e. the species with the maximum number of individuals). SR is species rank; *b* and *c* are estimated parameters.

Forest structure: cell based

Information about ecosystem structure presents a useful complement to the biological analysis of species richness and abundance patterns. A frst approach to characterizing structure

is to subdivide a study area into smaller cells (or quadrats). The subdivision into smaller spatial units facilitates detailed analysis of small-scale patterns, as well as comparison among diferent study areas. Figure [2](#page-4-0) presents a visual impression of the spatial species mix and the tree diameter at breast height (dbh) distribution in the three study areas. Some species are size dominant represented by large individuals: *Ficus benghalensis* in Bugarikallu; *Terminalia paniculata* and *Eucalyptus tereticornis* in Doresanipalya; *Ficus microcarpa, Terminalia arjuna, Premna tomentosa,* and *Albizia odoratissima* in Thalewoodhouse. The cell-based distributions of the following seven variables in each study area will be analysed:

BA_ha: basal area in m² per ha.

*N*_ha: number of woody plants per ha.

S: cell richness (number of species in cell).

Dq: quadratic mean dbh (cm).

CVD: dbh coefficient of variation.

M: cell Mingling (the ratio: number of species/number of individuals in cell).

CE: Clark & Evans index in cells.

The absolute discrepancy between the distributions of these variable in two study areas was calculated using the following criterion:

$$
d = \frac{1}{2} \sum_{i=1}^{m} |p_i - q_i|
$$
 (3)

where p_i and q_i are the relative frequencies in the *i*'th frequency class of a particular variable in pairs of study areas that we wish to compare. The absolute discrepancy d thus represents the proportion of a particular frequency in one study area that has to be changed such that both distributions (ordered by specifc frequency classes) are identical. Cells of size 20×20 m will be used for the analysis.

Forest structure: individual based

Forest structure may also be characterized by evaluating the immediate neighbourhood of selected tree species. The variables *Mingling, Dominance* an*d Size Diferentiation* will be used to describe the specific neighbourhood constellations of each individual species. Three measures of species-specifc structural diversity are defned as follows (Gadow [1993;](#page-14-10) Pommerening et al. [2020](#page-15-8)):

Fig. 2 General impression of the spatial species mix and tree dbh distribution in the three study areas. Each species is identifed by a unique colour across all three study sites. The big 100×100 m areas

The three variables represent a system for characterizing structural patterns at high resolution in a consistent set where all the variables assume values in the interval [0, 1]. *Mingling* defnes the degree of spatial segregation of the tree species (Gadow [1993](#page-14-10); Aguirre et al. [2003;](#page-14-11) Pommerening and Grabarnik [2019\)](#page-15-4). *Dominance* measures the size dominance of the reference tree in relation to its immediate surrounding (Hui et al. [1998](#page-14-12)). *Size Diferentiation* measures the variation in tree sizes between the reference tree and its nearest neighbours (Pommerening et al. [2020](#page-15-8)). Instead of selecting a particular reference species (as was done in this study), trees that belong to a particular family could be selected, or all dominant trees of a given species, as reference trees with the aim to study their particular neighbourhoods.

It is also seen that reference trees located close to the plot edge may produce a biased estimate of the neighbourhood constellation because some of the real nearest neighbours may be located outside, beyond the plot perimeter. To avoid such bias, edge correction has to be employed. The simplest method involves a defnition of a bufer around the plot edges. Edge correction, ensuring that the distance to the plot boundary of each reference tree must be greater than the distance to its 4th neighbour, is applied in this study to avoid biased estimates of the neighbourhood parameters.

Results

We present descriptive and modelling results in this section. Both allow detailed monitoring of the current diversity of woody plant species and forest structures, and thus an evaluation of the resilience and functioning of the three systems, over time. Such monitoring is essential for active conservation.

Woody plant species

The top 10 species by number of individuals are presented in Table [2.](#page-5-0) Appendix 1 presents a table with details for each species, separately for each study area. The information includes parameters that are assessed in routine forest inventories (mean dbh, trees per ha) as well as the means of the structural parameters Mingling (*M*), Dominance (*D*) and Size Diferentiation (*T*). A summary of the details in Appendix 1 is presented in Table [3.](#page-5-1)

The top 10 species occupy 75% of the total individuals in Bugarikallu, 69% in Thalewoodhouse and 89% in Doresanipalya. *Ixora arborea* with 333 individuals accounted for 15% of the abundance in Bugarikallu, *Olea dioica* with 292 individuals accounted for 18% abundance in Thalewoodhouse, and *Santalum album* with 791 individuals accounted for 38% abundance in Doresanipalya.

Almost 70% of all the tree and shrub species encountered in the three study sites occur on all three sites. Thirty one percent, (181–137) of 130, of species are not common to all three sites. (Table [3\)](#page-5-1)

Twenty-two species of climbers were found in the three permanent study areas (Table [4](#page-6-0)). Altogether 356 individual climbers belonging to 12 species occur in the Thalewoodhouse study area. Bugarikallu has 350 individual climbers belonging to 15 species while Doresanipalya has 272 climbing individuals belonging to 7 species. The dominant climber species in Thalewoodhouse are *Hiptage benghalensis*, a liana which is often found in the upper canopies, and two stragglers: *Ziziphus oenoplia* and *Jasminum angustifolium*.

The most frequent climbers in Bugarikallu are three stragglers: *Pterolobium hexapetalum*, *Jasminum angustifolium*

Table 2 List of top 10 species with number of individuals

Bugarikallu		Thalewoodhouse		Doresanipalya			
Species	Number of individuals	Species	Number of individuals	Species	Number of individuals		
Ixora nigricans	333	Olea dioica	292	Santalum album	791		
Anogeissus latifolia	249	Cipadessa baccifera	154	Shorea roxburghii	301		
Erythroxylum monogynum	238	Ziziphus oenoplia	139	Ziziphus oenoplia	208		
Pterolobium hexapetalum	169	Phyllanthus polyphyllus	134	Eucalyptus tereticornis	173		
Maytenus emarginata	130	Hiptage benghalensis	121	Dendrocalamus strictus	127		
Ochna obtusata	125	Ixora nigricans	106	Acacia auriculiformis	89		
Tarenna asiatica	116	Polyalthia cerasoides	74	Pterocarpus marsupium	61		
Acacia chundra	96	Ardisia solanacea	57	Breynia vitis-idaea	58		
Canthium dicoccum	95	Glochidion velutinum	45	Leucaena leucocephala	31		
Jasminum angustifolium	88	Jasminum angustifolium	40	Albizia lebbeck	27		
Table 3 Summary of the species-specific details listed in Appendix 1	Study Site	Tree, shrub & climber species	Number of families	Species per family	Number of species introduced/invasive		
	Bugarikallu	76	35	2.17	2		
	Doresanipalya	46	20	2.30	10		

Thalewoodhouse 69 28 2.46 1 3 Sites combined 130 40 3.25 11

and *Ziziphus oenoplia*. The endangered twiner *Decalepis hamiltonii* (IUCN Red list of Threatened Species) is also found in Bugarikallu. *Ziziphus oenoplia* is the most frequent climber in Doresanipalya followed by *Gymnema sylvestre,* a well-known medicinal plant.

Introduced/invasive species

Two non-native woody plant species occur in Bugarikallu (*Cassia siamea and Eucalyptus globulus*), ten in Doresanipalya (*Acacia auriculiformis, Anacardium occidentale, Annona squamosa, Cassia siamea, Cassia spectabilis, Eucalyptus tereticornis, Grevillea robusta, Jacaranda mimosifolia, Leucaena leucocephala,* and *Psidium guajava*) and one in Thalewoodhouse (*Cassia spectabilis*). Numerous rare species are found in each of the three study areas. Many rare species are only represented by one individual (refer to Appendix 1 for details).

Neighbourhood structure

Each tree species is characterized by an average dbh, a specifc contribution to the total density of woody plants, and by a species-specifc neighbourhood constellation. The relevant details are found in Appendix 1. The variable Mingling obviously assumes a maximum value of 1.0 for all species that occur with only 1 individual, e.g. *Acacia leucophloea*, *Atalantia* *monophylla, Carmona retusa, Cipadessa baccifera, Decalepis hamiltonii, Phyllanthus indofischeri* and several others in Bugarikallu. The mean Mingling values are low for species occurring with a high frequency (e.g. 0.45 for *Ixora nigricans* with 1033 individuals; 0.57 for *Anogeissus latifolia* with 546 individuals; 0.51 for *Pterolobium hexapetalum* with 400 individuals; 0.61 for *Canthium dicoccum* with 208 individuals) in Bugarikallu. Species occurring with a high relative frequency are likely to have more conspecific neighbours. *Premna tomentosa* and *Shorea roxburghii* in Bugarikallu, or *Glochidion zeylanicum* in Thalewoodhouse have low mingling values despite their low frequencies. Such unexpected constellations indicate spatial aggregation within conspecifc clusters.

Cell‑based Structure

The absolute discrepancies among the three study areas, based on the seven cell variables, are presented in Table [5.](#page-6-1)

Bugarikallu and Thalewoodhouse differ most in density (BA_n) , quadratic mean dbh (Dq) and diameter coefficient of variation (CVD). Bugarikallu and Doresanipalya difer in terms of species richness and diameter coefficient of variation. Doresanipalya and Thalewoodhouse difer most by density, richness, diameter coefficient of variation and cell mingling. The cellbased analysis combines small-grain measures of density and crowding, richness and size variation and can be used to assess the degree of similarity or dissimilarity among forest stands, or between a current and some ideal target structure.

Species	TW	BG	D _O	Characteristics
Acacia concinna	5	10	$\mathbf{0}$	Shrubby straggler with prickles (understorey & canopy)
Argyreia cuneata	0	2		Stout climbing shrub (understorey & canopy)
Argyreia sericea	0	$\mathbf{0}$	8	Stout Climber (on the ground, understorey & canopy)
Cansjera rheedei	0	3	0	Climber (canopy & understorey)
Capparis sepiaria	0	3	0	Scandent shrubs with spines (understorey & canopy)
Celastrus paniculatus		5	0	Straggling shrub (understorey)
Decalepis hamiltonii	Ω		0	Endangered Twining shrub (Rocks, understorey)
Embelia viridifolia	0	0		Woody climbers (understorey)
Gymnema sylvestre	$\mathbf{0}$	4	26	Twining subshrub (understorey & Canopy)
Hiptage benghalensis	121	0	0	Large woody climber-twiner (Upper canopy)
Ichnocarpus frutescens	14	$\mathbf{0}$	0	Climber (understorey $\&$ canopy)
Ipomoea illustris		0	0	Climber (understorey)
Jasminum angustifolium	40	88	0	Straggling shrub (understorey)
Mimosa rubicaulis	18	$\overline{0}$	0	Straggling shrub with prickles (understorey)
Pterolobium hexapetalum	0	169	$\mathbf{0}$	Prickly straggler (understorey)
Scutia myrtina		17	24	Spiny straggling shrub (understorey & canopy)
Secamone emetic	Ω		$\mathbf{0}$	Scandent shrubs (understorey & canopy)
Toddalia asiatica	2	8	0	Straggler with recurved prickles (understorey & canopy)
Tylophora indica	Ω	0	4	Slender pubescent climber (understorey & canopy)
Ventilago maderaspatana	11		$\mathbf{0}$	Woody climbing shrub (Upper canopy)
Ziziphus oenoplia	139	37	208	Scandent shrub with thorns (understorey)
Ziziphus rugosa	3		0	Straggling shrub with spines (understorey)
Total individuals (total species)	356(12)	350(15)	272(7)	

Table 5 Absolute discrepancies (0.60-0.70=60-70%, >0.70=>70%) among the three study areas, based on the seven cell variables that were used in this study

The species–area relation

The estimated parameters *a* and *b* of the monod model, and the graphs of the ftted functions for each feld plot, are presented in Table [6.](#page-6-2)

By solving the monod equation for any arbitrary area, an estimate of species richness for that area is obtained. The parameters in Table [6](#page-6-2) can thus be used to make species richness values comparable among diferent plot sizes.

Table 6 Estimated parameters a and b of the monod model for the three study areas

Study area	Species rich-	SAR (Monod)			
	ness	a	h		
Doresanipalya	46	0.04146	0.000816		
Bugarikallu	76	0.11790	0.001513		
Thalewoodhouse	69	0.02996	0.000449		

The species abundance distribution

Species abundance curves provide information about how communities differ in the way they are organized. The species abundance distribution generally takes a curve shape that is defned by many rare species and a few common ones (McGill et al. [2007](#page-14-13); Matthews et al. [2014](#page-14-14)). Figure [3](#page-7-0) presents the three graphs of the ftted SAD's.

The Weibull parameter b increases with increasing number of species and can be estimated by the following linear function: Weibull $b=-0.5862+0.3942$ *(number of species per ha). The parameter *b* was estimated by regression.

The shape of the species abundance distribution is infuenced by the degree to which common species dominate the community, and by the number of very rare species (McGlinn et al. [2019\)](#page-15-9). Communities that are strongly dominated by one or a few species often have low species diversity overall.

Discussion

Tree species richness and diversity

The importance of tree species diversity for forest functioning has led to the measurement of species diversity when compared to the traditional physical attributes (diameters, heights, crown dimensions) of individual trees, stands and forests. Accordingly, there is a rich literature on diversity, with many contradictory recommendations (Hubálek [2000\)](#page-14-15). Most popular are Hill's numbers as easily interpreted measures of diversity. This includes the exponential form of the Shannon function (Hill's *N*1) and the reciprocal of Simpson's index (Hill's *N*2). The choice depends on whether more weight is given to the rare species (*N*1) or to the common species (*N*2).

Traditional indices of biodiversity incorporate only the numbers of species and their frequencies without considering the biological diferences among the species. Ganeshaiah et al. [\(1997](#page-14-16)) proposed a measure of community diversity known as the "Avalanche index". The Avalanche measure, recently "revived" by Hao et al. ([2019a,](#page-14-17) [b](#page-14-18), [2021\)](#page-14-19), is defined as follows:

$$
A = \sum_{i=1}^{S} \sum_{j=i+1}^{S} p_i * d_{ij} * p_j
$$
 (4)

where *S* is the total number of tree species, p_i and p_j are the relative frequencies of species *i* and *j* in the community, and d_{ii} is a measure of the taxonomic distance between species *i* and *j*. The Avalanche diversity does not only account for the number of species and their frequencies, but also considers the taxonomic hierarchy. The Shannon entropy would be the same for two communities *A* and *B* if both have the same number of species occurring with the same frequencies. The Avalanche diversity in *B* would exceed that in *A* if the number of genera would be greater in *B* than in *A*, because the

Avalanche index captures the intra-community biological variation. The Avalanche is not only useful as an index of diversity, but also as a measure that can be used to assess the dissimilarity of two forest communities (Hao et al. [2019a](#page-14-17); see also Talents et al. [2005\)](#page-15-10). Table [7](#page-8-0) shows that the Hill D1 (the exponent of the Shannon index) is almost identical for *Bugarikallu* and *Thalewoodhouse* although *Bugarikallu* has more species than *Thalewoodhouse* but a lower evenness. This result is supported by the fact that the *Avalanche* index for *Thalewoodhouse* exceeds that for *Bugarikallu*. The number of species per family is 2.17 in Bugarikallu, and 2.46 in *Thalewoodhouse* (Table [2](#page-5-0)) which explains the slightly greater *Avalanche* value for *Thalewoodhouse*.

Species richness depends on plot size. One way to derive a common estimate of species richness is to develop a species–area relation (SAR) for each plot individually and to estimate richness for a particular standard area, such as 1 hectare. The results from this study thus provide a useful basis for comparison with other ecosystems, and for testing general assumptions presented in previous studies (e.g. Preston [1962;](#page-15-11) Hubbell [2001](#page-14-20)).

A quantity of considerable practical relevance is the minimum contiguous area required to capture all the species within a particular region. Gadow and Hui ([2007\)](#page-14-21) found a relationship, based on tree-mapped field plots assessed in various regions of the world, between the maximum number of tree species within a forest region (S_{max} , which is often known), and the minimum contiguous area required to capture all the species within that region (A_{min}) , measured in m²). The minimum contiguous area was estimated in that study by the function $A_{\text{min}} = 487.8 \cdot S_{\text{max}}^{0.524}$. This result implies that, for contiguous forest areas, the form of the species–area relationship is directly defned by the observed species abundance and the maximum number of species in the region. Assuming that the maximum number of species in the region around Bengaluru is 130, the

Fig. 3 Species abundance distributions of the three study areas. When plotted in this way, relative species abundances from very different data sets show similar patterns

Table 7 Species richness per ha and three measures of diversity: the Shannon entropy and its exponent value, Hill number D1 and the Avalanche index for the three plots

Study area	Trees, shrub, $\&$ climber species richness			Shannon Hill D1 Avalanche	
Doresanpalya	46	2.263	9.61	0.321	
Bugarikallu	76	3.078	21.71	0.345	
Thalewoodhouse 69		3.069	21.52	0.352	

estimate of the minimum contiguous area to capture all species would be $487.8*130^{\circ}0.524 = 6250.98$ m² in each of the three plots. This area is less than that of the study areas $(10,000 \text{ m}^2)$. An inspection of the graphs of the SAR functions reveals that this estimate is quite reasonable.

Specifc relationships

The structural parameters provide additional information about the close-range neighbourhood of each species. Not surprisingly, high correlation values are found between tree density and mingling for individual species. No relation was found regarding the dbh diferentiation (*T*). Tree dbh variation within neighbourhood groups was independent of tree dbh and the degree of species mingling.

The relationships between variables that are often assessed in routine forest inventories (mean dbh and number of trees), and neighbourhood parameters (Mingling and Dominance) are shown in Fig. [4](#page-9-0) for the three study areas. The relation between the number of trees per ha and the mean neighbourhood mingling is estimated using a power function. The relation between the mean dbh (cm) and the mean neighbourhood Dominance is estimated using the Monod function. Figure [4](#page-9-0) presents the graphs and the equations of these relationships for each study area.

Pro‑active conservation

The methods of analysis used in this study may be helpful in regions where complex multi-species forests require advanced methods for sustaining their resilience and functioning. We refer to these approaches as "pro-active conservation", in contrast with *laissez-faire* and neglect. Ecosystem resilience is the inherent ability to absorb various disturbances while maintaining critical functions. One factor that is known to increase resilience is species richness (Qiao et al. [2021\)](#page-15-12); another is structural complexity (Lian et al. [2022\)](#page-14-22). Pro-active conservation thus involves preventing loss of species richness (e.g. by eliminating aggressive invaders, or reducing the number of individuals of a very dominant species) and maintaining structural complexity.

To be able to do this, species richness and structural attributes need to be monitored in permanent observational study areas. Corrective action can be taken based on the analysis of the physical structure and the shape of the species abundance distribution.

Many of the world's forest ecosystems are used for several purposes, and these often include the potentially conficting goals of timber production and biodiversity conservation. Franklin et al. [\(1997\)](#page-14-23) proposed "variable retention" as a silvicultural concept that retains forest structural elements in order to preserve environmental values associated with structurally complex forests. This practice increases public acceptance by preserving key habitat components with benefts for tree-dwelling plants, wood-inhabiting insects and fungi. Puettmann et al. ([2015\)](#page-15-13) presented arguments in favour of the global acceptance of a set of principles that include avoidance of clear-cutting, emphasis on structural diversity and small-scale variability, deployment of mixed species with natural regeneration and avoidance of intensive site-preparation methods. Bauhus and Schmerbek ([2010](#page-14-24)) described various methods for creating and maintaining structural variability in commercial plantation forests by retaining patches of native vegetation. These examples reveal a general trend towards managing mixed temperate forests sustainably. Pro-active conservation of species-rich tropical forests is rather more challenging, however, than uneven-aged management of temperate forests, especially if the main objective is not sustained timber production, but sustained conservation.

Tropical forest vegetation is dynamic and highly irregular and is characterized by a set of tree species that may include a considerable proportion of non-native ones. Structures are highly complex. In theory, the degree of "naturalness" of an ecosystem is the diference between its current state, relative to some assumed "natural state". Ecosystems are, however, subject to continual change, even when they are protected from human use. Naturalness therefore is a "moving target". The "natural state" is something that cannot be defned. It is impossible to measure and objectively evaluate the degree of "naturalness", but it is possible to describe some aspects of the ecosystem that are known to be important for its functioning, such as the diversity of tree species. The dominance of invasive species, for example, may require active interventions, to modify the SAD to a fatter shape. Advanced analysis, as demonstrated in this study, provides the basic information that is needed for designing residual communities that maintain both the desired species mix (portfolio efects) and structure to ensure resilience and sustained functioning. The "Residual Basal Area" approach (see details in Gadow et al. [2021,](#page-15-14) p 307 et sqq.) may be a practical alternative for pro-active conservation of such ecosystems.

Modelling long‑term stand dynamics

In view of sustainable use and adaptive management in response to assumed environmental change, modelling longterm stand dynamics has been high on the list of research

Fig. 4 Relationships between species-specifc variables in the three plots. Shown are the number of trees per ha and the mean neighbourhood mingling with the estimated non-linear model below

(upper row); the mean dbh (cm); and the mean neighbourhood dominance with the estimated monod model (below)

priorities. Of particular interest are new compatible models of tree growth and forest production. Linking models with diferent levels of resolution is the key to simultaneous estimation of individual tree growth and survival, and forest production (see detail in Cao and Struba [2008;](#page-14-25) Hevia et al. [2015;](#page-14-26) Gadow et al. [2021](#page-15-14), p 258). To obtain such data requires repeated assessments of change, e.g. for estimating tree growth, mortality and recruitment. Such data have been collected in Europe for long periods of time (Pretzsch et al. [2015,](#page-15-15) [2017;](#page-15-16) Seifert et al. [2014](#page-15-17); Álvarez-González et al. [2009](#page-14-27); Albert et al. [2015](#page-14-28); Gadow et al. [2021](#page-15-14)), but are often scarce or absent in many regions of the world. We are committed to remeasuring the study areas used in this analysis for estimating tree growth, mortality and recruitment, and the changes in biodiversity over time, and in response to a changing climate.

Conclusions

Despite their importance, tropical dry forests are among the most threatened and least studied of the world's forested ecosystems and, as a result, are at even greater risk of disappearing than humid forests, primarily due to higher population densities and the associated demand for energy and land. Surprisingly, despite their great value in providing essential services, these forests have received relatively little research attention. Much of the data required for policy is absent or incomplete. This study aims to fll that gap using observations from the South Indian Deccan Plateau by providing essential information for pro-active conservation based on a detailed analysis of the biological and finescale structural characteristics of 130 woody plant species, including a great variety of climbers. The new methods presented in this study facilitate comparison between observed and desirable forest structures, and the selection of efective strategies for pro-active conservation.

Appendix

See Table [8](#page-10-0).

Table 8 Species tagged in the three permanent preservation plots

Species	meanD	meanH	N	BA	mean M	mean D	mean T	mean CV
Thalewoodhouse								
Acacia concinna	5.8	$\mathbf{0}$	8	0.03	0.78	0.78	0.4	0.46
Albizia odoratissima	37.9	13	$\mathbf{1}$	0.11	$\mathbf{1}$	$\mathbf{1}$	0.9	$\mathbf{1}$
Allophylus cobbe	2.6	3.5	12	0.01	0.91	0.52	0.34	0.47
Ardisia solanacea	2.9	2.7	134	0.11	0.4	0.45	0.38	0.55
Bauhinia racemosa	3	\overline{c}	2	$\boldsymbol{0}$	$\mathbf{1}$	0.63	0.32	0.5
Breynia retusa	2.2	$\overline{2}$	\overline{c}	0	$\mathbf{1}$	0.75	0.31	0.51
Breynia vitis-idaea	2.1	2.5	$\mathbf{1}$	$\mathbf{0}$	$\mathbf{1}$	0.5	0.47	0.63
Butea frondosa	17.5	6	$\mathbf{1}$	0.02	1	1	0.87	$\mathbf{1}$
Canthium dicoccum	1.8	3	$\mathbf{2}$	$\boldsymbol{0}$	0.75	0.38	0.31	0.48
Canthium parviflorum	2.6	2.8	10	0.01	0.88	0.4	0.39	0.47
Careya arborea	12.5	11	3	0.04	0.83	0.92	0.73	0.97
Cassia fistula	5.5	5.1	32	0.14	0.8	0.55	0.48	0.6
Cassia spectabilis	6.3	6	1	$\boldsymbol{0}$	1	1	0.61	0.56
Celastrus paniculatus	1.1	$\overline{0}$	1	$\mathbf{0}$	$\mathbf{1}$	$\overline{0}$	0.65	0.49
Cipadessa baccifera	1.9	2.3	404	0.13	0.34	0.47	0.32	0.45
Cordia wallichii	9.4	6.5	31	0.26	0.94	0.89	0.64	0.78
Dalbergia lanceolaria	21.6	15.2	8	0.49	0.91	0.78	0.74	0.85
Dendrocalamus strictus	2.5	2.5	3	$\boldsymbol{0}$	0.83	0.5	0.4	0.47
Dimocarpus longan	1.5	1.5	$\mathbf{1}$	0	$\mathbf{1}$	$\mathbf{0}$	0.4	0.26
Diospyros melanoxylon	8.8	4.1	$\overline{4}$	0.03	1	0.63	0.34	0.38
Diospyros montana	6.8	6	17	0.1	0.97	0.67	0.49	0.69
Embelia tsjeriam-cottam	2.1	1.9	8	0	0.34	0.41	0.37	0.6
Ervatamia heyneana	1.5	1.5	$\mathbf{1}$	0	$\mathbf{1}$	$\boldsymbol{0}$	0.55	0.86
Erythrina stricta	11.1	8	$\mathbf{1}$	0.01	1	1	0.69	0.85
Erythroxylum monogynum	$\mathbf{2}$	2.9	4	0	0.88	0.13	0.59	0.88
Ficus microcarpa	50.3	25	10	3.6	0.03	0.6	0.59	0.99
Flueggea leucopyrus	1.6	\overline{c}	1	0	1	0	0.64	0.65
Garuga pinnata	1.6	\overline{c}	1	$\boldsymbol{0}$	1	0	0.49	$\mathbf{1}$
Glochidion velutinum	6.1	5.9	119	0.52	0.37	0.51	0.43	0.63
Glochidion zeylanicum	5.2	3.7	31	0.14	0.48	0.58	0.47	0.62
Gmelina arborea	18.3	14	\overline{c}	0.06	$\mathbf{1}$	0.88	0.53	0.61
Grewia tiliifolia	1.6	$\mathfrak{2}$	$\mathbf{1}$	0	1	0.25	0.28	0.31
Helicteres isora	2.2	3.3	4	0	0.75	0.56	0.35	0.34
Hiptage benghalensis	5.3	$\boldsymbol{0}$	183	0.61	0.69	0.55	0.46	0.64
Holarrhena antidysenterica	3.8	2.3	\overline{c}	$\boldsymbol{0}$	$\,1$	0.25	0.38	0.58
Ichnocarpus frutescens	$2.4\,$	$\boldsymbol{0}$	19	0.02	0.83	0.22	$0.5\,$	0.76
Ipomoea illustris	1.8	$\boldsymbol{0}$	$\mathbf{1}$	$\boldsymbol{0}$	$\,1$	0.75	0.17	0.15
Ixora nigricans	$2.8\,$	$2.8\,$	151	0.12	0.74	0.48	0.44	0.63
Jasminum angustifolium	2.3	$\boldsymbol{0}$	46	0.02	0.95	0.29	0.45	0.61
Mallotus philippensis	4.8	4.4	26	0.1	0.45	0.52	0.46	0.74
Maytenus emarginata	2.2	1.5	2	$\boldsymbol{0}$	0.75	0.75	0.32	$0.8\,$
Memecylon umbellatum	3.1	4.4	7	0.01	0.5	0.64	0.42	0.54
Miliusa tomentosa	6	5.1	6	0.03	0.67	0.75	0.54	0.73
Mimosa rubicaulis		$\boldsymbol{0}$	31		0.73	0.42	0.33	0.43
	2.5			0.02				
Mitragyna parvifolia Olea dioica	12.5 4.9	10.1 4.5	9 517	0.18	0.31	0.61	0.58	0.82
				2.19	0.55	0.52	0.42	0.57
Pavetta indica	$\mathbf{2}$	2.9	16	0.01	0.77	0.27	0.49	0.59
Phyllanthus emblica	6.5	5.6	$\,8\,$	0.06	0.93	0.64	0.46	0.54
Phyllanthus polyphyllus	\mathfrak{Z}	3.8	479	0.48	0.29	0.53	0.35	0.45
Phyllanthus reticulatus	4.6	2.7	5	0.01	0.75	0.55	0.41	0.84

Table 8 (continued)	Species	meanD	meanH	$\mathbf N$	BA	mean M	mean D	mean T	mean CV
	Ficus benghalensis	27.71	10	11	0.72	0.14	0.57	0.33	0.4
	Ficus microcarpa	91.99	9	$\mathbf{1}$	0.66	$\mathbf{1}$	$\mathbf{1}$	0.94	$\mathbf{1}$
	Flacourtia indica	3.24	2.95	50	0.06	0.79	0.46	0.42	0.55
	Flueggea leucopyrus	$3.8\,$	$\overline{\mathcal{A}}$	$\mathbf{1}$	$\boldsymbol{0}$	1	0.75	0.35	0.44
	Gardenia turgida	1.1	1.5	$\mathbf{1}$	$\boldsymbol{0}$	1	0.25	0.22	0.33
	Grewia asiatica	6.76	6	2	0.01	0.75	0.88	0.5	0.61
	Grewia hirsuta	1.1	1.5	$\mathbf{1}$	$\boldsymbol{0}$	1	$\boldsymbol{0}$	0.69	0.48
	Grewia orbiculata	3.06	2.84	82	$0.08\,$	0.69	0.44	0.42	0.51
	Gymnema sylvestre	1.78	$\boldsymbol{0}$	$\overline{4}$	$\boldsymbol{0}$	1	0.31	0.32	0.47
	Holarrhena antidysenterica	3.12	3.11	49	0.05	0.67	0.58	0.42	$0.52\,$
	Ixora nigricans	3.2	3.07	1033	1.02	0.45	0.53	0.35	0.43
	Jasminum angustifolium	1.7	$\boldsymbol{0}$	145	0.04	0.83	0.27	0.43	0.57
	Lagerstroemia parviflora	6.34	4.75	20	0.08	0.65	0.7	0.4	0.49
	Madhuca indica	7.46	5.87	19	0.14	0.39	0.62	0.4	0.47
	Maytenus emarginata	2.23	2.29	319	0.15	0.48	0.43	0.37	$0.5\,$
	Memecylon umbellatum	2.46	5	11	0.01	0.41	0.48	0.42	0.52
	Naringi crenulata	5.34	4.5	$\overline{4}$	0.01	0.94	0.88	0.51	0.67
	Ochna obtusata	3.74	3.23	215	0.27	0.61	0.52	0.37	0.45
	Phyllanthus indofischeri	11.62	7	$\mathbf{1}$	0.01	$\mathbf{1}$	$\mathbf{1}$	0.75	0.88
	Polyalthia cerasoides	3.81	3.86	18	0.03	0.97	0.57	0.47	0.56
	Polyalthia coffeoides	2.55	2.88	$\overline{4}$	$\mathbf{0}$	0.69	0.5	0.51	0.56
	Premna tomentosa	3.06	3.22	25	0.02	0.39	0.5	0.39	$0.4\,$
	Pterocarpus marsupium	9.5	6.06	8	0.07	$\mathbf{1}$	0.84	0.71	0.91
	Pterolobium hexapetalum	2.08	0.01	400	0.17	0.51	0.43	0.34	0.47
	Randia dumetorum	2.45	2.26	27	0.02	0.61	0.34	0.41	0.49
	Rapanea wightiana	7.32	5	\overline{c}	0.01	0.75	0.88	0.35	0.33
	Santalum album	2.56	3.67	3	$\mathbf{0}$	$\mathbf{1}$	0.17	0.4	0.62
	Scolopia crenata	5.09	6	$\mathbf{1}$	$\mathbf{0}$	$\mathbf{1}$	0.75	0.35	0.45
	Scutia myrtina	2.14	$\boldsymbol{0}$	35	0.02	0.72	0.39	0.39	0.49
	Secamone emetica	$1.5\,$	$\boldsymbol{0}$	$\mathbf{1}$	$\mathbf{0}$	$\mathbf{1}$	$\boldsymbol{0}$	0.39	0.41
	Semecarpus anacardium	13.53	6.75	6	0.09	0.75	0.88	0.59	0.79
	Shorea roxburghii	5.06	5.5	12	0.03	0.33	0.63	0.44	0.49
	Soymida febrifuga	8.65	5.75	\overline{c}	0.01	$\mathbf{1}$	$\mathbf{1}$	0.57	0.72
		8.06	6.63	$\overline{4}$	0.03	0.88	0.69	0.6	0.67
	Stereospermum suaveolens	6.44	3.78	9	0.04	0.89	0.56	0.53	0.63
	Strychnos potatorum Tarenna asiatica	1.77	2.62	313	0.09	0.56	0.33	0.39	0.53
	Terminalia chebula	9.44	6.97	15	0.11	0.72	0.8	0.56	$0.7\,$
					$0.03 \quad 1$				0.73
	Terminalia paniculata	8.52	5.5	$\overline{4}$			0.81	0.62	
	Toddalia asiatica	1.63	$\boldsymbol{0}$	10	$\boldsymbol{0}$	0.95	0.23	0.42	0.46
	Ventilago maderaspatana	3.7	$\boldsymbol{0}$	5	0.01	0.75	$0.8\,$	0.33	0.52
	Vitex altissima	5.19	6.33	12	0.03	0.67	0.65	0.46	0.59
	Wrightia tinctoria	6.65	7.5	6	0.05	0.13	0.75	0.55	$\mathbf{1}$
	Ziziphus oenopolia	2.19	0.29	62	0.03	0.71	0.35	0.43	0.56
	Ziziphus rugosa	2.9	$\boldsymbol{0}$	$\mathbf{1}$	$\boldsymbol{0}$	$\mathbf{1}$	$\boldsymbol{0}$	0.36	0.22
	Ziziphus xylopyrus	2.4	$3.5\,$	4	$\boldsymbol{0}$	0.88	$0.5\,$	0.49	0.41
	Doresanipalya								
	Acacia auriculiformis	9.5	7.4	117	1.32	0.55	0.66	0.56	0.73
	Albizia amara	6	8	\overline{c}	0.01	0.75	0.5	0.63	0.83
	Albizia lebbeck	11.2	5.4	33		0.54 0.85	0.77	0.6	$0.78\,$
	Albizia odoratissima	4	$3.5\,$	$\mathbf{1}$	$\boldsymbol{0}$	1	0.75	0.32	0.34
	Anacardium occidentale	5.2	$2.8\,$	23		$0.08\quad 0.12$	$0.58\,$	0.41	0.52

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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