On the patterns of tree diversity in the Western Ghats of India

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We have explored in the Western Ghats the patterns of tree diversity in relation to vegetation types which have been primarily defined on the basis of structure and phenology. A total of 20,785 individuals, belonging to 398 species, were enumerated along 108 belt transects covering a total area of 75 ha, from localities that spanned the entire length of the hill chain of the Western Ghats (8°N to 21°N latitude and 73°E to 75°E longitude) in peninsular India. These transects were assigned to 7 vegetation types and were shown to be distinctive in species composition. These types include closed canopy evergreen, semi-closed canopy evergreen, stunted evergreen, semievergreen, moist deciduous, dry deciduous forests, and scrub/savanna vegetation. Dry deciduous forests with low levels of density and diversity harbour a rather exclusive set of species. The most diverse tree assemblages belong to the semievergreen forest type, which harbours widespread species extensively shared with other vegetation types. The semiclosed evergreen forests resemble semievergreen forests in many ways. In contrast, the stunted evergreen forests and scrub/savanna exhibit low values of tree density and diversity; their component species have very weak tendencies to co-occur with each other. The evergreen and moist deciduous forests exhibit moderate to high density and diversity and moderate levels of distinctiveness of species composition. The evergreen forests however resemble dry deciduous forests in harbouring species with a strong tendency to co-occur and many species with restricted distributions. More moist vegetation types shelter a higher proportion of evergreen and endemic trees and a lower proportion of medicinally-useful species. These results have significant implications for devising a sampling strategy.

THE 1990s have witnessed an upsurge of interest in the patterns of distribution of biological diversity as a result of technological developments which have opened up many possibilities of utilization of such diversity, and new regimes of sovereign rights of countries of origin over biodiversity, ushered in by the Convention on Biological Diversity[1] (CBD). CBD commits parties to the Convention, amongst them India, to take an inventory of their biodiversity resources, and to organize programmes of regular monitoring, especially to assess the efficacy of conservation measures[2]. Wild relatives of cultivated plants are amongst the resources CBD mentioned as of particular interest. India is an important centre of these resources, which are particularly concentrated in the Western Ghats tract[3]. The Western Ghats has also been identified as a 'hot spot' – an area of high levels of diversity, also under considerable threats[4]. Inventorying and monitoring of the biological diversity of the Western Ghats is therefore an important challenge before the community of systematists, biogeographers and ecologists of India[5].

This is an enormous challenge, for the Western Ghats harbour around 5500 species of flowering plants alone[6]. Globally, flowering plants are estimated to constitute 2.5% of the total number of species of all groups[1]; this leads to an estimate of 2,20,000 species over the Western Ghats. The complex mosaics of habitats created as a result of human interventions give rise to very intricate patterns of distribution of organisms on the Western Ghats[7]. It is our endeavour to explore and understand these patterns[8,9].

Forests constitute the natural climax vegetation over most of the Western Ghats; an understanding of the distribution of tree species and their assemblages must therefore play an important role in elucidating the larger patterns of distribution of biodiversity. These distributions are governed by factors such as rainfall, slope, aspect and soils; by biotic interactions such as grazing by herbivores, and by a variety of human interventions such as biomass harvests, fire and planting of economic species. The resultant complex distributions of the 800 or so tree species of the Western Ghats[10] have been captured in terms of the distributions of assemblages assigned to a small number of classes termed forest types, vegetation types or vegetation series. While we have qualitative information like lists of species characteristic of different categories of these various classification systems, there have been inadequate systematic quantitative investigations of these classification systems. Our preliminary investigations report the following: (i) Its starting point is the recognition of seven structural–phenological classes of vegetation types

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largely following the French Institute[11], Indian Forestry Research[12] and UNESCO[13] systems. (ii) The extent to which classes recognized on the basis of structure and phenology vary in terms of species composition. Specifically we are interested in the variation in species composition amongst different samples assigned to the same class, in contrast to different classes. (iii) Levels of α- and β-diversity in samples from the various classes. (iv) Apart from these attributes of individual or pairs of assemblages we are interested in other attributes which can be computed from larger sets of assemblages. These include measures of how prevalent species making up an assemblage are and the extent to which they occur together. (v) We have introduced some new ways of looking at these issues and apply them to the tree assemblages of the Western Ghats.

Materials and methods

Western Ghats, the focus of our studies, comprise of a chain of hills 1600 km in length running parallel to the west coast of the Indian peninsula, with a width from 5 km to 150 km and elevations rising up to 2800 m (ref. 6). The higher elevations support a restricted number of vegetation types; the great majority of types being extensively distributed at lower elevations[11]. Western Ghats supports an elaborate mosaic of vegetation types, and our samples are based on 108 transects each confined to a relatively homogeneous patch of a single vegetation type at 30 localities with elevations ranging from sea level to 1200 m. For our purpose we distinguish 7 vegetation types on the basis of structure – physiognomic and phenological attributes. Table 1 specifies their correspondence with the typologies suggested by Champion and Seth[12], Pascal[11] and UNESCO[13].

Champion and Seth[12] provide a structural–phenological classification framework, but neglect the more human impacted vegetation types, and consider some of the vegetation types as belonging to subtropical climatic zone, a view which is no longer widely held[14]. Within this framework, Pascal[11] has carefully identified various human impacted categories, and we use some of them. However, within each structural category he proposes several geographically separated series of plant communities, identified on the basis of dominant species of the potential climax. We have not adopted such a fine classification as the species composition changes more or less continuously even in adjacent localities within a given structural type. Further, as potential climax forests are restricted to a very small area, it is best to design a practicable system to classify the vegetation that exists, as permitted by the prevalent levels of human influence, all over the Western Ghats. The typology we propose is as follows:

1) Evergreen forests comprise tall trees (25–30 m in height), with erect, closed, dense canopy covering nearly 95% of the ground (by canopy we mean overall vegetal cover, not just the top canopy). Due to the gaps in the top canopy that occupy up to 10% of the forest area, complete canopy closure is not possible. Nearly all – 90% or more trees belong to evergreen species. Leaves are thick, dark or blackish green and shining. Barks of many trees are smooth. Many trees have large buttresses. Lianas, i.e. woody climbers are not uncommon. Undergrowth is almost devoid of herb species. Thorny species are few, mainly canes and pandanus, which are common.

2) Semiclosed evergreen forests have tall trees (20–25 m in height), and partially closed (80–95%) canopy. 80% to 95% trees belong to evergreen species. Although the canopy is much more closed than in the case of semievergreen or deciduous forests, we have used the term semiclosed only to distinguish these from highly closed canopy evergreen forests. Because of the canopy openings in the past, a few herbaceous species and many pioneer woody species, including some deciduous ones, inhabit the forest floor. Lianas, especially canes, are common. Thorny species, including canes, are not uncommon.

3) Stunted evergreen forests have dwarf trees, 10–15 m in height with a closed (80–95%) canopy. Over 80% of the trees are evergreen. The trees often branch at the base and have a spreading canopy. Buttressed trees are rare or absent. Lianas are very abundant. The forests are rich in undergrowth of pioneer shrubs like *Strobilanthes*, which have thin, hairy leaves. Thorny species are not uncommon, but canes and pandanus are rarely present.

4) Semievergreen forests have a mixture of moderately tall evergreen and deciduous trees, 15–20 m in height, and closed (60–80%), dense canopy. About 40–80% trees are evergreen. Unlike the closed and semiclosed evergreen forests, many trees lack straight, tall boles and have an irregular canopy. Herbaceous species are not uncommon on the forest floor and climbers grow in profusion. Lianas are common. Canes are uncommon and pandanus rare.

5) Moist deciduous forests have moderate, tall trees (10–20 m in height), and closed but not very dense canopy (40–70%). 0 to 40% trees are evergreen. The deciduous species tend to shed their leaves early, around January. Trees have rough bark; mostly thin, pale green leaves. Buttressed stems are rare. Undergrowth contains many herbaceous species. Occasionally, there is extensive growth of weeds like *Lantana* or *Eupatorium*. Lianas are very few, but climbers are common. Thorny species are not uncommon, but canes and pandanus are not present.

6) Dry deciduous forests have tall trees of 10–15 m in height with a rather open (40–60%) canopy. Evergreen and buttressed trees are not present. Lianas are rare. Thorny species are common, but canes and pandanus are

Table 1. The correspondence between vegetation types amongst various classification systems

Proposed type	Champion and Seth[12]	Pascal[11]	UNESCO[13]
Evergreen forests	West coast tropical evergreen forests, 1.A.C4	Lowland wet climax evergreen forests	Tropical lowland broadleaved seasonal evergreen forests, I.A.2.a.1
Semi-closed evergreen forests	Same as above	Disturbed lowland wet evergreen forests	Same as above
Stunted evergreen forests	Western subtropical broadleaved hill forests, 8.A.C.2	Stunted submontane evergreen forests	Tropical broadleaved seasonal evergreen submontane/cloud forests, I.A.2.e.1
Semievergreen forests	West coast tropical semievergreen forests, 2.A.C.2	Secondary semi-evergreen forests	Tropical lowland broadleaved semideciduous forests, I.A.3.a.1
Moist deciduous forests	Southern tropical moist deciduous forests 3.B.C/S.1/2	Secondary/climax moist deciduous forests	Tropical broadleaved drought deciduous forests I.B.1.a.1
Dry deciduous forests	Southern tropical dry deciduous forests, 5.A.C.1/2/3	Secondary/climax dry deciduous forests	Same as above
Scrub/savanna	Seral stages like Euphorbiaceous scrub, 1/2/3/5/8.S/DS.1/2/3	Scrub woodlands tree savannas	Tropical broadleaved drought deciduous: woodlands, II.B.1.a.1; scrub, III.B.1.a.1; short-grass savanna, V.A.2.a.2

Note: Pascal[11] assigns the entire Western Ghats to the tropical climatic zone, departing from the classical approach by Champian and Seth[12]. We adopt Pascal's view. UNESCO system[13] uses the terms tropical and subtropical, but does not separate numbers types therein.

not present. Herbaceous and grassy undergrowth, sometimes including weeds is plentiful.

7) Scrub/savanna are non-forest formations, having shrubby (scrub) or grassy (savanna) undergrowth with a scattered tree canopy (0–40%). Trees show variable heights from 5 to 15 m. Proportion of evergreen trees varies from place to place, depending upon the climate and successional status. However, deciduous trees are generally more common. Lianas are absent. Thorny species and herbs, including weeds are common.

Sampling of the tree assemblages is generally based on transects or quadrates, covering 1000 m^2 area, and hence comprising only 20 to 60 individuals[7]. Recent investigations point to the need of sampling at least 100 individuals, preferably in several replicates at a given locality[15]. We therefore aimed at sampling at least 100 trees with diameter at breast height (DBH) of 130 cm of 10 cm or more in each sampling event. The sampling area was therefore permitted to vary, involving a transect of a fixed width of 20 m and length varying from 135 m to 825 m, with a mean of 383 m. Thus, the total area covered for the 108 samples was 75 ha. In 8 out of 108 transects, we failed to reach the target of 100 individuals, so that the number of trees sampled per transect ranged from 89 to 691, with a mean of 197. The field sampling was conducted by GU, who assigned the 21,285 trees sampled to 398 operational taxonomic units (OTUs). Of these 398 OTUs, 370 were assigned to species level, 8 to genus level, and the remaining 20 to morphospecies, on the basis of their vegetative characters[16]. There is a strong possibility that the 8 OTUs assigned to genus level, and 5 of the 20 OTUs identified as morphospecies may each include several species with highly local distributions that are difficult to discriminate on the basis of vegetative characters alone, and for which flowers or fruits could not be procured during the field work. The number of species recorded on a single transect varied from 8 to 87.

Of the 7 vegetation types recognized and sampled, evergreen, moist deciduous and dry deciduous forest types are distributed throughout the Western Ghats. The

Table 2. Sampling effort according to latitudinal zones and vegetation types

Latitude degree N		Closed evergreen forest	Semiclosed evergreen forest	Stunted evergreen forest	Semi-evergreen forest	Moist deciduous forest	Dry deciduous forest	Scrub/ savanna	No. of transects.	No. of sites
8–10		3	7	1	3	3	2	5	24	6
10–12		10	2	1	9	4	2	1	29	9
12–14		2	3	1	8	1	–	10	25	4
14–16		2	–	1	–	1	–	–	4	2
16–18		5	–	9	4	2	–	–	20	5
18–21		1	–	1	–	2	2	–	6	4
Total		23	12	14	24	13	6	16	108	30
									Total	
Length m	mean	329	489	275	357	397	479	352	387	
	s.d.	76	336	75	165	176	209	125	185	
Area m^2	mean	6227	6285	5500	7146	7942	9575	6538	7222	
	s.d.	1615	3043	1500	3298	3523	4171	2647	3184	
Trees	mean	253	215	157	179	216	161	133	197	
	s.d.	96	100	58	42	67	36	45	80	
Species	mean	38	48	23	40	27	27	28	33	
	s.d.	14	15	7	14	10	4	12	11	

tall, semi-closed evergreen forests are largely not present in the northern region, i.e. Maharashtra, where there is a tendency for development of stunted evergreen forests under conditions of disturbance. As a result, samples of semiclosed evergreen forests were restricted to latitudes between 8° and 14°N, and those of stunted evergreens largely to latitudes between 17°N and 18°N. The sampling of scrub/savanna was also restricted to the zone between 8°N and 14°N due to logistic constraints, although this type of vegetation extends further north as well. Table 2 provides further details of distribution of these transects and study areas across the latitudinal gradient and vegetation types.

We have characterized the 108 assemblages of trees thus sampled in six ways.

(i) α-diversity of species encountered in a given sample may be measured merely as species richness, or in terms of indices such as Shannon–Weaver or Simpson's index. Since the values of such possible indices are very strongly correlated to species richness[8], we have adopted a simpler measure of richness in subsequent discussion. However the number of species is strongly influenced by the number of individuals sampled, which varies from 89 to 691. We have corrected for this variation by rarefaction, through arriving at the expected number of species amongst 89 randomly selected individuals[17].

(ii) β-diversity is related to the proportion of unshared species in comparing two sets of species, and was measured as dissimilarity of species composition, d_{jk} amongst two samples j and k. It is defined in terms of the chord distance, which reflects the relative difference between two transects as projected onto a circle of unit radius[17].

$$d_{jk} = \left[1 - \left(\sum_{i=1}^{s} x_{ij}x_{ik}\right) \Big/ \left(\sum_{i=1}^{s} x_{ij}^2 \sum_{i=1}^{s} x_{ik}^2\right)^{1/2}\right]^{1/2},$$

where x_{ij} and x_{ik} are the numbers of individuals of species i in transects j and k respectively, and s is the total number of species encountered over the two transects j and k.

(iii) This dissimilarity has been specified in two ways, for all pairs of transects assigned to a given vegetation type, and for all pairs in comparing transects assigned to two different vegetation types. The level of dissimilarity in composition amongst any pairs of transects would be expected to increase with geographical distance between the transects. We have attempted to remove this effect by also computing within and between type dissimilarities using geographically proximate sites defined here as sites within 1 degree of latitude from each other. If the assignment of transects on the basis of structure–phenology is accompanied by occurrence of a characteristic set of species then across type levels of dissimilarity should be greater than those within types. This has been characterized by the ratio of mean dissimilarity of a type for all pairs across types to mean dissimilarity of all pairs within a given type. This ratio has been termed as the *distinctiveness* of a given type.

(iv) Members of any given species may occur on several of the transects sampled. A particular set of species encountered on a given transect may then be characterized by the mean proportion of transects on which members of the set are encountered. To facilitate comparison amongst studies involving different numbers of assemblages sampled, an index – called prevalence – has been suggested by us and is defined as:

$$p_i = \frac{\sum_{j=1}^{m_i} f_{ij}}{m_i},$$

where p_i is the prevalence for transect i, f_{ij} is the proportion of the total number of transects, n, over which a species j present on the transect i is encountered, and m_i is the total number of species encountered on transect i. Prevalence will then vary between $1/n$ and 1; a value close to 0, implying none of the species encountered on that transect was encountered elsewhere; a value of 1 implying that all the species encountered on a given transect were found on all the other transects. The lower the value of prevalence, the more restricted in distribution is the set of species found in that transect.

(v) The term cohesiveness has been used to characterize the extent of cohesion of species in any particular assemblage. It is computed in relation to the affinity, i.e. departure of the mean of overlap for all pairs of species in that assemblage, from the overlap expected on the basis of chance alone. The overlap A_{ij} between any pair of species may be computed as: $A_{ij} = T_{ij}/(T_i + T_j - T_{ij})$; where T_{ij} is the number of transects over which i and j occur together, and T_i, T_j are the number of transects over which species i and j occur respectively. Thus, computed overlap is dependent on sampling effort, being underestimated by low levels of sampling. The value of overlap expected by chance alone is $C_{ij} = p_i p_j/(p_i + p_j - p_i p_j)$; where $p_i = T_i/T$ and $p_j = T_j/T$; T being the total number of transects. The departure of the overlap from that expected on the basis of chance is therefore $A_{ij} - C_{ij}$. This correction renders the overlap measure independent of level of sampling effort. The expected value of this quantity, the affinity is 0 if the probability of occurrence of species i on any transect is independent of the probability of occurrence of species j on that transect. If there is a positive tendency for the two species to occur together, then A_{ij} will take a positive value between 0 and 1; if the occurrence of i implies a lower than random chance of the presence of j, then it will take a negative value between 0 and 1. It should be noted that the second term correcting for expected co-occurrence on the basis of chance alone would have a high value if both species are widespread, and a low value if both are rare. Cohesiveness is defined as:

$$V = \frac{\sum_{i=1}^{n-1} \sum_{j=i+1}^{n} A_{ij} - C_{ij}}{((n^2 - n)/2)},$$

where n is the total number of species present on the transect. It would take a high value if the constituent species have a high degree of affinity amongst themselves, making up a cohesive set of species. It will take a low value if the constituent species are derived as if by chance from many different assemblages, and have little affinity for each other.

These two indices, prevalence and cohesiveness attempt to define properties relating to diversity at the level of sets of species assemblages, namely, how widespread and cohesive species constituting the assemblages are. This goes beyond the normal measures of diversity such as species richness characterizing single assemblages[8]. Cohesiveness is not a trivial consequence of diversity, but an independent property negatively correlated to prevalence, i.e. how widespread the species in an assemblage are. It is useful to examine whether the cohesiveness of the observed assemblages differs significantly from those of simulated random assemblages. We have done so on the basis of three kinds of assumptions: (i) All 398 species have an equal chance of occurring on any of the transect, with the total number of species per transects fixed between 8 and 87, with 10 simulations of each level of species richness; (ii) one hundred simulations setting the distribution of species richness per transect as observed, and (iii) one hundred simulations setting the distribution of prevalence per species as observed. It turns out that the observed range as well as standard deviation values of cohesiveness are significantly different from that of random assemblages created in any of these three ways. The observed mean is higher than in simulated assemblages, implying that real life tree assemblages do exhibit a measure of cohesion. Furthermore, the standard deviation of cohesiveness in observed assemblages is significantly greater, implying that the variation in extent of cohesion is of real ecological significance. We also carried out one further check, namely, deleting the species which occur on only one or two transects. It turns out that the computed cohesiveness values do not differ significantly from those computed by retaining the whole species set.

Unlike species diversity or evenness, cohesiveness has no meaning as a property of single assemblages. Instead it depends on the distribution of tree species over a number of assemblages. It is then necessary to check the minimum number of assemblages for which the value of cohesiveness stabilizes. To do so the mean cohesiveness was computed for different numbers of assemblages for assemblages drawn randomly from the pool of observed assemblages. The value of cohesiveness quickly rises up to 15 transects and reaches an asymptote around 50 transects. With a sample of 108 assemblages, we are well above this limit.

(vi) We also computed the proportions of total trees present in each transect that belonged to the species of medicinal importance[18], wild relatives of cultivated plants[3], those endemic to the Western Ghats[19], and those having evergreen foliage[11], on the basis of specification of these attributes in the literature, for the species under consideration.

Further, the correlation coefficients were calculated between the various environmental and diversity parameters of the 108 transects. For characterizing the vegetation types in terms of their various attributes, the mean value of each attribute was computed for each vegetation type at the transect level. To furnish an idea of characteristic and commoner species of various vegetation types, the species were grouped into those that were confined to a single vegetation type, shared between two, three and so on up to all the seven types. From each of these seven groups of species, seven species were chosen such that each had its peak frequency of occurrence in a different vegetation type resulting in the selections of a total of 49 species. One more widespread species was then added to this set. These 50 species and the vegetation types were then arranged on the basis of their reciprocal averaging scores[20].

Results and discussions

As Table 3 shows the within type average β-diversity between transects is invariably lower than that across types, confirming that the types identified by us as different on the basis of structural considerations also differ significantly in terms of constituent species, although the latter has not been served as the basis of classification of the vegetation. Nagendra and Gadgil[21] have also demonstrated that these vegetation types can be reliably identified on the basis of supervised classification of satellite imagery as well. This implies that these vegetation types are an appropriate basis for a two-phase programme of biodiversity inventory, involving regional scale monitoring of land cover in terms of vegetation types coupled to point sampling of biological diversity levels in selected landscapes[1]. Table 4 lists the 50 most characteristic species of the 7 vegetation types on the basis of proportion of transects inhabited. These 50 species have been so chosen as to represent a wide range of distribution patterns, from those confined to a single type to those inhabiting all the types. Table 5 summarizes the values of various diversity parameters and attributes of these vegetation types.

Of these 7 vegetation types, the semievergreen and semiclosed evergreen forest types are amongst the least distinctive in composition. They are also richest in the α- and β-diversities, as measured by the mean of number of species in a given transect, as well as levels of species dissimilarity amongst pairs of transects of the same type. Correlated with this are rather high levels of prevalence and low level of cohesiveness, implying that these forest types constitute assemblages of widespread species with little affinity to each other. These two types are derived from the original evergreen type by moderate levels of disturbance in the form of selective harvesting of trees and incursion of more widespread, pioneer species, including deciduous species in the openings thus created.

The low altitude stunted evergreen forests of northern Western Ghats have resulted through re-colonization by pioneer species, following clearfelling of evergreen forests mostly for shifting cultivation[7]. A relatively restricted number of hardy species seem to have successfully done so, so that constituents of stunted evergreen

Table 3. Dissimilarity in the species composition within and across types

Vegetation type	No. of transects	ceg 22	sce 13	ste 14	seg 23	mdc 14	ddc 6	ssv 16
ceg	Allover	0.87	0.91	0.94	0.95	0.99	1.00	0.98
	1°N	0.84	0.91	0.91	0.93	0.99	1.00	0.98
sce	Allover		0.90	0.95	0.93	0.98	1.00	0.96
	1°N		0.90	0.93	0.91	0.98	1.00	0.96
ste	Allover			0.82	0.93	0.97	1.00	0.96
	1°N			0.81	0.90	0.95	1.00	0.94
seg	Allover				0.90	0.92	0.99	0.92
	1°N				0.89	0.89	0.99	0.90
mdc	Allover					0.87	0.93	0.89
	1°N					0.83	0.87	0.98
ddc	Allover						0.76	0.98
	1°N						0.67	0.98
ssv	Allover							0.82
	1°N							0.78

Note. We have given here the average values of chord distance between all the pairs of transects belonging to similar and different vegetation types. The distance depends on species abundance. The upper figures within each cell denote the values between pairs of transects distributed all over the Western Ghats, while the lower figures correspond to values between pairs of transects situated within one degree latitudinal distance. The values within type are always lower than across the types. ceg, closed canopy evergreen forests; sce, semiclosed canopy evergreen forests; ste, stunted evergreen forests; seg, semievergreen forests; mdc, moist deciduous forests; ddc, dry deciduous forests; ssv, scrub/savanna.

Table 4. 50 most characteristic species and the 7 vegetation types arranged in the order of the reciprocal averaging scores

	Code		1	2	3	4	7	5	6				
Family	Vegetation type Species	Rav	ceg 0	sce 5	ste 11	seg 20	ssv 41	mdc 56	ddc 100	Peak type	No.of types	No.of ind.	No.of trans.
Dipterocarpaceae	*Hopea erosa*	0	9							2	1	42	2
Euphorbiaceae	*Baccaurea courtallensis*	3	32	38						1	2	55	12
Clusiaceae	*Mesua nagassarium*	3	27	38						2	2	84	11
Anacardiaceae	*Holigarna nigra*	5		23						2	1	9	3
Burseraceae	*Canarium strictum*	5	45	38		13				1	3	45	18
Meliaceae	*Aglaia elaeagnoidea*	5	45	69		17				2	3	234	23
Myristicaceae	*Knema attenuata*	6	95	69	29	22	6			1	5	396	40
Lauraceae	*Beilschmiedia dalzellii*	7	50	31	36	26				1	4	96	26
Meliaceae	*Harpullia arborea*	8	27			17				4	2	14	10
Rutaceae	*Atlantia racemosa*	9			29			7		3	1	9	5
Lauraceae	*Litsea stocksii*	9	18		57	4				4	3	141	13
Anacardiaceae	*Holigarna grahamii*	9	36	15	43	30				3	4	229	23
Sapindaceae	*Dimocarpus longan*	9	73	69	36	43	13			2	5	687	42
Lauraceae	*Actinodaphne angustifolia*	10	5		71					3	2	66	11
Moraceae	*Artocarpus lakoocha*	10	18	54		22	6			2	4	25	17
Tetramelaceae	*Tetrameles nudiflora*	13	5	31		43				3	3	53	16
Lauraceae	*Persea macrantha*	14	64	38	7	39	13	14		1	6	138	33
Dipterocarpaceae	*Hopea parviflora*	15	32	62	7	30	25	7		2	6	311	28
Lauraceae	*Cinnamomum* spp.	15	41	77	29	43	38	7		2	6	167	40
Anacardiaceae	*Mangifera indica*	19	41	62	50	74	25	36		4	6	286	51
Melastomaceae	*Memecylon umbellatum*	19	23	8	79	13	31	14		3	6	433	27
Oleaceae	*Olea dioica*	20	36	54	86	74	63	29		3	6	718	58
Euphorbiaceae	*Macaranga peltata*	21	50	46	29	74	31	43		4	6	381	50
Euphorbiaceae	*Mallotus philippensis*	21	18	46	29	61	25	29		4	6	172	36
Sapotaceae	*Xantolis tomentosa*	23	5		57	17	13	21		3	5	109	19
Myrtaceae	*Syzygium cumini*	23	27	15	86	26	56	29		3	6	256	40
Verbenaceae	*Vitex altissima*	26	9	54		61	31	43		4	5	179	34
Dilleniaceae	*Dillenia pentagyna*	34		23		48	56	43		7	4	185	30
Lytheraceae	*Lagerstroemia microcarpa*	37	14	54	14	65	44	79	33	5	7	335	48
Combretaceae	*Terminalia paniculata*	38	14	23		61	94	57	17	7	6	952	45
Rubiaceae	*Wendlandia notoniana*	41					25			7	1	21	4
Mimosaceae	*Xylia xylocarpa*	44				22	13	50		5	3	309	15
Sapindaceae	*Schleichera oleosa*	44		31		57	25	64	33	5	5	179	32
Combretaceae	*Terminalia bellirica*	45	14	31	7	57	25	71	50	5	7	158	39
Lecithydaceae	*Careya arborea*	47		15	14	26	75	50	33	5	6	227	32
Tiliaceae	*Grewia tiliifolia*	52		8	7	52	31	50	50	6	6	244	29
Apocynaceae	*Wrightia tinctoria*	56						14		5	1	2	2
Euphorbiaceae	*Bridelia retusa*	58	5	8	14	4	63	71	67	6	7	93	30
Combretaceae	*Terminalia crenulata*	62				26	56	57	67	5	4	317	28
Papilionaceae	*Pterocarpus marsupium*	62				26	75	79	83	6	4	244	34
Euphorbiaceae	*Phyllanthus emblica*	63	5	8			63	57	67	7	5	61	24
Verbenaceae	*Tectona grandis*	67				13	19	50	50	4	4	388	16
Apocynaceae	*Holarrhena antidysenterica*	69					19		17	7	2	6	4
Rubiaceae	*Morinda tinctoria*	72						29	17	5	2	15	5
Sapotaceae	*Madhuca latifolia*	72					31	29	50	7	3	81	12
Papilionaceae	*Butea monosperma*	83					13	21	67	6	3	35	9
Combretaceae	*Anogeissus latifolia*	85			7	4	6	14	100	6	5	273	11
Celastraceae	*Cassine glauca*	92						14	67	6	2	13	6
Euphorbiaceae	*Givotia rottleriformis*	100							67	6	1	17	4

ceg, closed canopy evergreen forests; sce, semiclosed canopy evergreen forests; ste, stunted evergreen forest; seg, semievergreen forests; mdc, moist deciduous forests; ddc, dry deciduous forests; ssv, scrub/savanna. No. of types, Number of vegetation types inhabited; No. of ind., Total number of individuals; No. of trans., Number of total transect inhabited; Peak type, The vegetation type code where the species attains peak frequency; Rav, Reciprocal Averaging Values.

forests exhibit moderately high levels of prevalence and cohesiveness, coupled to moderate levels of distinctiveness. Levels of α- and β-diversity as measured by species richness and within type dissimilarities are also very low.

Scrub/savannas are widely distributed over the Western Ghats, created through high levels of harvests and incidence of fire. In the high rainfall zone they are derived from the original evergreen vegetation. These constitute highly heterogeneous environments permitting

Table 5. Attributes of transects according to the various vegetation types

Vegetation types		1 ceg	2 sce	3 ste	4 seg	5 mdc	6 ddc	7 ssv
Environmental attributes								
Latitude	mean	13.7	11.0	16.5	13.3	13.8	13.5	12.1
(degree N)	s.d.	3.0	1.8	3.0	2.8	4.1	5.4	2.2
Length of dry season	mean	5.6	4.5	6.7	5.5	5.8	6.7	5.2
(months)	s.d.	1.2	0.8	1.0	1.0	1.5	0.9	0.9
Average annual rainfall	mean	4704	3308	5043	3467	2400	1267	3344
(mm)	s.d.	1191	1416	1240	1349	1081	335	1366
Average altitude	mean	607	654	875	417	342	358	638
(m ASL)	s.d.	162	273	238	188	219	291	307
Diversity attributes								
Tree density/ha	mean	419	365	340	302	276	243	191
	s.d.	169	143	197	124	61	56	115
α-diversity	mean	27	35	18	30	23	20	21
	s.d.	8	7	6	6	8	5	6
β-diversity	mean	1.17	1.14	1.11	1.19	1.17	0.76	1.07
	s.d.	0.13	0.06	0.2	0.08	0.12	0.15	0.18
Distinctiveness	mean	1.14	1.17	1.19	1.14	1.14	1.84	1.24
cohesiveness	mean	0.11	0.09	0.09	0.07	0.09	0.15	0.08
	s.d.	0.03	0.03	0.02	0.01	0.02	0.02	0.02
Prevalance	mean	0.16	0.15	0.18	0.20	0.18	0.08	0.22
	s.d.	0.03	0.04	0.04	0.04	0.05	0.02	0.04
Evergreenness (%)	mean	95	90	81	66	28	14	35
	s.d.	6	6	17	18	14	11	25
Endemicity (%)	mean	55	46	23	32	12	2	18
	s.d.	13	11	16	16	9	2	14
Medicinal trees (%)	mean	30	28	39	36	62	81	53
	s.d.	14	7	19	12	16	7	16
Wild relatives of	mean	27	27	32	26	22	17	25
cultivated plants (%)	s.d.	13	8	12	9	18	7	13

ceg, closed canopy evergreen forests; sce, semiclosed canopy evergreen forests; ste, stunted evergreen forests; seg, semievergreen forests; mdc, moist deciduous forests; ddc, dry deciduous forests; ssv, scrub/savanna.

Table 6. Correlation between various attributes of diversity and environment for the transects

Attribute	Code	1 lat	2 rain	3 veg	4 ind	5 alp	6 chv	7 prv	8 evg	9 edm	10 med	11 wrc
Latitude	lat		**0.40**	–0.07	–0.02	**–0.31**	–0.08	**0.26**	0.14	–0.01	0.04	0.22
Rainfall	rain			**–0.47**	0.00	0.05	–0.15	**0.32**	**0.62**	**0.44**	–0.16	0.10
Vegetation type	veg				–0.13	**–0.32**	–0.02	0.09	**–0.67**	**–0.53**	**0.32**	0.00
Individuals	ind					0.19	–0.02	–0.18	–0.03	0.01	–0.02	0.03
α-Diversity	alp						–0.23	–0.21	0.19	**0.32**	**–0.25**	–0.00
Cohesiveness	chv							**–0.57**	–0.07	–0.15	0.07	–0.07
Prevalence	prv								0.13	0.03	–0.11	0.07
Evergreenness	evg									**0.63**	**–0.30**	–0.01
Endemicity	edm										**–0.36**	0.00
Medicinal plants	med											–0.01
WRCP proportion	wrc											

Values significant at $P < 0.01$ are printed in bold type while those significant at $P < 0.05$ are underlined. Critical values of $r(df = 106)$: 0.185 ($P < 0.05$), 0.240 ($P < 0.01$).

the coexistence of species with divergent requirements. In consequence, these species assemblages are fluid, with very low levels of cohesiveness and high levels of prevalence. However, a relatively limited number of hardy species successfully colonize scrub/savanna, so that the assemblages are moderately distinctive but exhibit rather low levels of α- and β-diversities.

Evergreen forests, the climax vegetation in the high rainfall zone of the Western Ghats harbour highest levels of tree densities with moderate levels of α- and β-

diversities as well as distinctiveness. The moist deciduous forests, the climax formation in the medium rainfall zone exhibit much lower tree densities and lower levels of cohesiveness in comparison with the evergreen type, but resemble the latter in being moderately distinctive with moderate levels of α- and β-diversities and prevalence.

The other natural climax vegetation type of the Western Ghats, the dry deciduous forest of the lower rainfall tracts is by far the most distinctive in composition. It has rather low tree densities, and low levels of α-diversities. The assemblages have the lowest levels of prevalence and highest levels of cohesiveness, with a rather constant composition so that β-diversities are the lowest of all types. However, if one computes various parameters based on the data from just 6 transects per type so as to ensure uniform sampling intensity across types, the closed canopy, climax evergreen forests replace the dry deciduous forests in possessing the highest cohesiveness and lowest prevalence values.

Table 5 further shows that the closed canopy evergreen forests rank the highest in the proportion of trees belonging to endemic species of the Western Ghats, often more than half of the total trees in a trasect. While the dry deciduous forests have poor representation of the endemic species, over 80% of the trees often belong to species of medicinal importance. The semiclosed canopy evergreen forests have the lowest proportion of medicinal species, less than a third of the total trees. The proportion of trees belonging to wild relatives of cultivated plants remains nearly the same across all the types, i.e. one fourth, with dry deciduous forests having the lowest values and stunted evergreen forests the highest.

Table 6 shows that while prevalence and cohesiveness do not depend on the vegetation type, α-diversity is negatively and prevalence is positively correlated with latitude ($P < 0.01$), and in turn with the length of the dry season. The prevalence is also negatively correlated with the cohesiveness. α-diversity is negatively correlated ($P < 0.01$) with the rank aridity of the vegetation characteristic of the types, assigned on the basis of literature[11]. Increasing evergreenness of the forest corresponds to increasing endemicity ($P < 0.01$), but is accompanied by a significant ($P < 0.05$) reduction in proportion of medicinally valuable trees.

The degree of prevalence and co-occurrence of species characteristic of certain vegetation types might be expected to depend upon the relative allocation of sampling efforts to those types. To correct for the possible distortion of results due to unequal sampling efforts, we computed all the indices for each vegetation type on the basis of 6 transects chosen from 4 localities close to those of the dry deciduous forest, which represented the lowest sampling effort. The results were very similar to those obtained by using the total data set with the overall ranking pattern remaining the same, although ranks of some of the consecutive types were interchanged in case of some parameters. In terms of actual values, the α-diversity values of the two sets of transects were highly significantly ($r = 0.96$, $P < 0.01$) correlated and prevalence values were significantly ($r = 0.75$, $P < 0.05$) correlated while the values for the β-diversity, distinctiveness and cohesiveness are not significantly correlated. We may then repose the highest level of confidence in the patterns of species richness and prevalence.

Our analysis provides a basis for arriving at the distribution of sampling effort at the landscape level in a programme of inventorying and monitoring biodiveristy. The details would of course depend on the specific objectives, for instance, if these involve maximizing the number of species encountered per unit effort, then greater effort may be devoted to vegetation types such as semiclosed evergreen forests with highest levels of α- and β-diversities. These results also have implications for conservation efforts. Again, if the objective is to maximize the number of protected species, the focus may be on disturbed vegetation types such as semiclosed evergreen forests. However, our interest may lie in conserving relatively rare species. Thus, vegetation types such as dry deciduous or closed canopy tall evergreen forests harbouring a rather cohesive set of species with restricted distributions may be given high priority. There are, of course, other considerations in according conservation priorities, such as occurrence of a given element outside the study area. For instance, the evergreen forests occur only in the Western Ghats, Northeast India, and Andaman and Nicobar Islands, and hence deserve higher priority than the dry deciduous forests that are extensively distributed in all other parts of the country. We have discussed the topic of conservation evaluation in detail elsewhere[9].

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ACKNOWLEDGEMENTS. We thank all the members of the Western Ghats Biodiversity Network for their local support. We thank the Ministry of Environment and Forests, Government of India and the local forest department officials for their continued co-operation. The PEW foundation is acknowledged for providing flexible financial support towards this endeavour. S. Srinidhi provided valuable programming support and P. Pramod participated in many useful discussions.

Received 7 August 1997; revised accepted 13 July 1998