

# On the hospitality of Western Ghats habitats for bird communities

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Species assemblages have been characterized in terms of numbers of individuals or various measures of diversity such as species richness or evenness. We may characterize sets of such assemblages in terms of how widespread their constituent species are and how cohesive the assemblages are. In this paper we define measures of these properties termed ubiquity and hospitality respectively. We explore the distribution of these two parameters, as well as the more commonly used measures of diversity for a set of 132 bird assemblages censused with the help of one hour long transects of 100 m × 500 m to 600 m in 21 localities covering 9 major types of habitats from across the entire length of the hill chain of Western Ghats in peninsular India. We find that while biological parameters characterizing individual transects are positively correlated amongst each other, various measures of ubiquity and hospitality form a distinct group of parameters positively correlated with each other, and physical parameters such as latitude and rainfall form a third independent group of positively correlated parameters. Hospitality and ubiquity thus turn out to be independent parameters providing biologically useful insights. For instance, montane evergreen forests and monoculture plantations both harbour species poor communities. However those of montane evergreen forests are cohesive assemblages of restricted geographical distributions, while those of monoculture comprise species of widespread occurrence drawn from many different habitat types.

CONSERVING the evolutionary heritage of diversity of life on earth is one of the major challenges of the day. Much as we would like to conserve the entire spectrum of genes, species, biological communities and their habitats, it is clear that choices will have to be made and certain components accorded higher priorities in the conservation effort. Leaving genes aside for the moment, such prioritization will have to be based primarily on attributes of species. In particular, species that are rare, either because of their narrow geographical range, narrow habitat preferences or low levels of local populations throughout would have to be given higher priorities<sup>1</sup>.

In this investigation we explore one particular facet of this issue, namely the distribution of species that may be identified as rare (as opposed to widespread) species in the bird assemblages of the Western Ghats region, identified as one of the 18 biodiversity hot spots of the world<sup>2</sup>. We also ask whether bird assemblages are totally random, being constituted as if by chance from species drawn from a larger pool, or whether certain sets of species have a significantly higher tendency for co-occurrence, either because of a common habitat preference, or a history of co-evolution<sup>3-5</sup>. Furthermore, we are interested in the question of whether there are assemblages in which a large number of rare species tend to co-occur with a high degree of regularity. If that is the case then these assemblages would assume considerable significance. It would then be important to identify the habitats of such assemblages and ensure that these are given a high priority in conservation efforts. We carry out such an exploration and conclude that montane evergreen or shola forests of higher altitudes of the Western Ghats are indeed such a habitat harbouring a cohesive assemblage of relatively rare species.

## Ubiquity and hospitality

To address these questions, we need measures of an attribute at the species level, namely extent of rarity, and an attribute at the assemblage or community level, namely extent of cohesion, or, constancy of co-occurrence of constituent species. We term the former attribute, extent of rarity (or being widespread) of a species as ubiquity. For the present purpose we characterize it as the number of bird transects sampled by us from the Western Ghats in which a species has been recorded. We use the term hospitality to characterize the extent of cohesion of species in any particular assemblage. This is computed as follows:

The overlap  $O_{ij}$  between any pair of species  $i$  and  $j$  may be computed as:

$$O_{ij} = T_{ij} / (T_i + T_j - T_{ij}),$$

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. This index

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is same as the Jaccard index. Next the value of  $C_{ij}$ , the overlap expected by chance alone, i.e. if species  $i$  and  $j$  were to occur independently of each other is given by

$$C_{ij} = p_i p_j / (p_i + p_j - p_i p_j),$$

where  $p_i = T_i/T$  and  $p_j = T_j/T$ ;  $T$  being the total number of transects. We now define affinity  $A_{ij}$  as the departure of observed overlap from the overlap expected by chance, i.e.

$$A_{ij} = O_{ij} - C_{ij}.$$

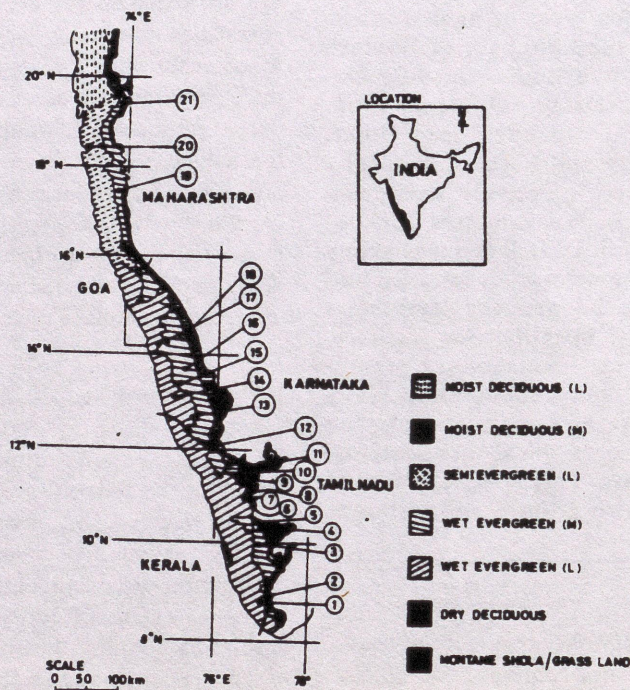
This measure is independent on the level of sampling effort, unlike  $O_{ij}$ . Since both  $(1 - O_{ij})$  and  $(1 - C_{ij})$  vary between 0 and 1, the affinity  $A_{ij}$  can vary from -1 to +1. The affinity between species  $i$  and  $j$  will be zero if they occur independently of each other, and will take a positive value if they tend to occur together. If occurrence of  $i$  implies a lower than random chance of the presence of  $j$ , affinity takes a negative value. It should be noted that  $C_{ij}$ , the overlap by chance alone will have

a high value if both species are widespread, and a low value if both are rare.

Since  $A_{ij}$  would be a measure of affinity or similarity, its value ranges from -1 to 1,  $-A_{ij}$  would be a measure of dissimilarity, which would also vary from -1 to 1, and we define hospitality as

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

where  $n$  is the total number of species present of the transect. Hospitality would then take a low value if the constituent species have a high degree of affinity amongst themselves, constituting a cohesive set of species. It will take a high value if the constituent species are derived as if by chance from many different assemblages, and have little affinity for each other. As we will see below, the primary montane evergreen shola assemblages turn out to be cohesive, harbouring species with



**Figure 1.** Sampling locations. Latitude, mean altitude, and mean rainfall in parentheses. 1, Bonakkad (8°38', 300 m, 250 cm); 2, Cuttlam (9°, 1200 m, 150 cm); 3, Pooyamkutti (10°08', 200 m, 300 cm); 4, Eravikulam (10°20', 2100 m, 400 cm); 5, Topslip (10°26', 800 m, 180 cm); 6, Walayar (10°50', 100 m, 200 cm); 7, Dhoni (10°52', 200 m, 200 cm); 8, Meenvallom (10°57', 400 m, 400 cm); 9, Upper Bhavani (11°15', 1800 m, 200 cm); 10, Muthappanpuzha (11°20', 400 m, 400 cm); 11, Mudumalai (11°50', 1000 m, 200 cm); 12, Makuta (12°, 500 m, 500 cm); 13, Subrahmanya (12°70', 300 m, 400 cm); 14, Mala (13°20', 600 m, 400 cm); 15, Kigga (13°24', 1000 m, 400 cm); 16, Neerelakoppa (13°35', 600 m, 300 cm); 17, Badal (14°20', 200 m, 250 cm); 18, Sirsi (14°33', 600 m, 250 cm); 19, Koyna (17°30', 800 m, 600 cm); 20, Phansad (18°25', 300 m, 400 cm); 21, Kalsubai (19°25', 800 m, 600 cm).

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Table 1. Mean and standard deviation of 13 transect level attributes in different habitats

Habitat categories	Total	M	E	F	D	S	P	H	R	
Number of transects	132	11	24	13	23	17	13	23	5	
Number of birds/transect	Mean	75.65	56.09	68.12	66.53	84.6	72.44	52.3	106.08	68.4
	s.d.	44.84	17.01	23.97	28.63	39.61	39.50	38.39	70.85	20.55
Number of species/transect	Mean	18.16	14.09	18.46	18.92	18.96	17.88	13.46	21.39	19.00
	s.d.	5.96	4.14	4.92	4.25	5.32	6.53	5.61	6.55	4.69
Rarefied species richness (sp./11 ind.)	Mean	7.03	6.37	7.13	7.40	6.94	7.02	6.58	7.27	7.64
	s.d.	0.96	0.92	0.90	0.83	0.94	0.88	1.14	0.83	0.48
Exponential Shannon-Weaver index	Mean	11.45	8.92	11.88	12.69	11.52	11.40	8.63	12.76	13.34
	s.d.	3.81	2.33	3.79	3.52	3.64	4.05	3.00	3.64	2.91
Simpson index	Mean	8.22	6.23	8.55	9.40	8.22	8.10	6.37	8.96	9.83
	s.d.	3.16	1.48	3.34	3.41	3.22	3.09	2.59	3.00	1.62
Fisher's alpha	Mean	8.43	6.42	8.84	9.57	7.91	8.05	7.93	9.33	9.46
	s.d.	2.95	2.36	2.95	3.12	2.06	2.30	4.54	2.37	3.08
Evenness of species abundance	Mean	0.68	0.67	0.67	0.70	0.66	0.67	0.70	0.66	0.72
	s.d.	0.11	0.11	0.10	0.09	0.13	0.11	0.14	0.11	0.04
1-Proportion of most abundant species	Mean	0.27	0.31	0.26	0.23	0.28	0.28	0.32	0.25	0.22
	s.d.	0.11	0.07	0.11	0.08	0.12	0.10	0.11	0.10	0.03
Mean hospitality of a transect	Mean	-0.05	-0.12	-0.05	-0.05	-0.04	-0.05	-0.04	-0.05	-0.07
	s.d.	0.03	0.04	0.01	0.01	0.01	0.02	0.01	0.02	0.02
Median hospitality of a transect	Mean	-0.04	-0.09	-0.04	-0.04	-0.03	-0.04	-0.03	-0.04	-0.05
	s.d.	0.02	0.05	0.01	0.01	0.01	0.01	0.00	0.02	0.02
Mean ubiquity for all sp. of a transect	Mean	31.18	20.98	34.55	34.56	33.99	32.98	31.23	28.98	22.65
	s.d.	7.50	5.54	4.59	5.16	5.60	8.95	5.51	6.88	4.36
Median ubiquity/transect	Mean	25.44	12.59	29.63	28.85	28.15	27.62	23.92	24.11	19.70
	s.d.	8.24	3.49	5.26	6.11	6.24	10.91	6.63	6.07	5.40
Standard deviation of ubiquity	Mean	23.01	22.48	23.82	24.76	23.71	23.61	25.11	20.68	17.18
	s.d.	4.30	7.13	2.76	2.11	3.24	3.23	4.89	4.04	2.78

M, Montane evergreen shola forests with natural grasslands; E, Evergreen forests which include stunted evergreen forests of northern Western Ghats; F, Semi-evergreen forests; D, Moist and dry deciduous forests; S, Scrub/Savanna; P, Monoculture plantations (rubber, eucalyptus, wattle, tea and coffee); H, Gardens and avenues around habitation; R, Paddy fields.

on an average low levels of ubiquity and characterized by low values of hospitality. In contrast, man-made monoculture plantations such as rubber and eucalyptus tend to harbour species with on an average high levels of ubiquity and exhibit high values of hospitality. These two proposed measures, ubiquity and hospitality attempt to capture properties relating to diversity at the level of sets of species assemblages, in contrast to the commoner approach of looking at measures of diversity such as Shannon-Wiener index at the level of single assemblages.

### Materials and methods

#### Bird assemblages

The investigation centres on the hill chain of Western Ghats that runs parallel to the west coast of India over a distance of 1600 km. This is a tract of heavy rainfall, originally covered extensively by humid tropical forest. Its current landscape is a highly variegated mosaic of natural and managed ecosystems<sup>6</sup>. A total of 508 species of birds were reported from south western India which include 144 species of water birds also<sup>7</sup>. Our data is based on belt transects of between 500 m and 600 m in length covered at an even pace over a one-hour period

between 0600 and 1000 h. Each transect passed through a patch of relatively homogeneous habitat. A transect involved recording of numbers of individuals of all birds sighted within 50 m on either side. A total of 132 such transects were undertaken between October 1995 and April 1996 in a total of 21 localities across the length of the Western Ghats (Figure 1). They involved a sighting of a total of 9987 birds belonging to 212 species. Water birds and the nocturnal birds were not sampled unless they occur by chance in the morning transects of the selected terrestrial habitats. The number of individuals sighted on a transect ranged from 11 to 259, with a mean of 75.7 and the number of species from 6 to 36, with a mean of 18.2. The number of transects on which a given species occurred ranged from 1 to 94, with a mean of 31.2. The resultant matrix of 212 species into 132 sites of relatively homogeneous patches of habitats furnishes us with the basic data set. Each of these sites may be assigned to one of the nine habitat categories (see Table 1).

### Results and discussions

This data set permits us to compute a series of standard parameters like diversity indices<sup>8-10</sup> along with ubiquity

and hospitality characterizing each transect as given in Table 1. Habitat categories based on structural characteristics of plants may not necessarily support distinctive bird assemblages. We have explored this issue on the basis of computations of pairwise chord distances using chord index<sup>11</sup> between all pairs of transects. It turns out that the mean within category chord distance was lower than the mean with respect to all remaining categories in only three cases, namely, sholas, evergreen forests and paddy fields. In all other cases the mean distance with one or more of other categories was lower than within category. The most poorly distinctive bird assemblages in this fashion are those of monoculture plantations. In this case the mean within category distance (0.942) is greater than the mean distance in relation to evergreen forests (0.896), deciduous forest (0.901), semi-evergreen forest (0.905), scrub-savanna (0.921), grasslands (0.936) and gardens (0.939).

#### Attributes of bird assemblages

Table 1 depicts the mean and standard deviation of values of the 13 transect level attributes for the 9 habitat categories. Two of the forest formations, sholas and monoculture plantations are similar in harbouring low numbers of birds and low diversity assemblages. However, while the mean ubiquity of bird assemblages of sholas is low, that of monoculture plantations is high. Correlated with this is the very low hospitality of sholas, and high hospitality of monoculture plantations. In other words, sholas harbour low diversity, but cohesive assemblages of species of restricted occurrence, while monoculture plantations also harbour low diversity bird assemblages, but of widespread species, that occur in many other types of habitats as well. This substantiates Daniels *et al.*'s<sup>12</sup> observation that monoculture (Eucalyptus) plantations have a larger proportion of generalist species.

A notable contrast is provided by the habitat types, gardens and paddy fields. These habitats harbour both large numbers of individual birds along with large number of species. At the same time, the mean ubiquity of species is lower than that of all types except shola. This implies that gardens and paddy fields have a core set of species restricted to these habitat types. In consequence, the hospitality is also rather low, suggesting that the assemblages of garden and paddy field birds are rather cohesive.

#### Correlations amongst transect attributes

It is of interest to examine the internal correlations amongst the values of 13 attributes computed for the 132 transects; and in particular to assess whether the new measure, that of hospitality is closely related to

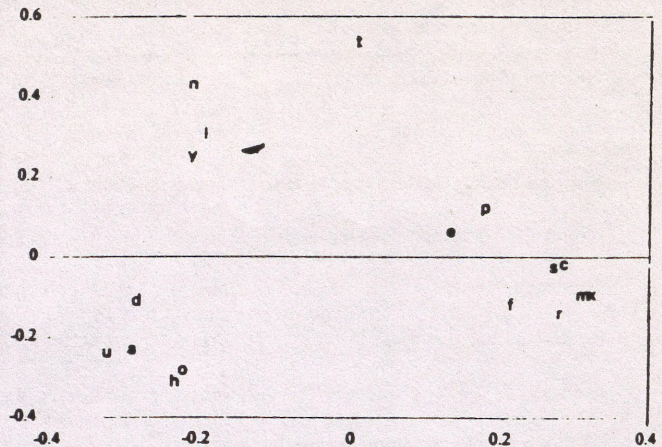


Figure 2. Two-dimensional representation of 13 transect level community attributes and 4 site attributes. u, Mean ubiquity; a, Median ubiquity; d, Standard deviation of ubiquity; h, Mean hospitality; o, Median hospitality; e, Evenness; p, Population of birds; f, Fisher's alpha; s, Species richness; c, Proportion of dominance; r, Rarefaction to 11 individuals; m, Simpson's index; x, Exponential of Shannon Wiener index; t, Altitude; n, Rainfall; l, Latitude; y, Number of dry months.

some of the more standard parameters. Figure 2 displays these correlations in the form of a 2-dimensional scatter plot, obtained using metric multi-dimensional scaling analysis. The eight measures characterizing assemblages individually in terms of numbers of individuals and species diversity are positively correlated with each other and form a group on the right hand side. In contrast, the five parameters characterizing sets of assemblages, namely mean (and median) hospitality and mean (and median) and standard deviation of ubiquity are positively correlated with each other and lie together in the lower left quarter. Apart from these 13 parameters derived from the abundances of bird species, each transect may also be characterized by its altitude, latitude, rainfall and number of dry months. These are correlated amongst each other because the higher altitudes of Western Ghats occur towards lower latitudes and because rainfall decreases and number of dry months increases with latitude. In this 2-D scaling plot, these four physical parameters form a separate group in the upper left quarter. These physical parameters then do not correlate with community attributes like diversity and hospitality.

It is then clear that hospitality is not a trivial consequence of diversity, but an independent property positively correlated to ubiquity, i.e. how widespread the species in an assemblage are. It is useful to examine whether the hospitality of the observed data differs significantly from those of simulated random assemblages. We have done so on the basis of three kinds of simulations: (i) All 212 species have an equal chance of oc-

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curing on any of the transects, with the total number of species per transect fixed between 11 and 30, 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 ubiquity per species as observed. It turns out that the observed range as well as standard deviation of hospitality is significantly different from that of random assemblages created in any of these three ways. The observed mean is lower than in simulated assemblages, implying that real life bird assemblages do exhibit a measure of cohesion.

Furthermore, the standard deviation of hospitality in observed assemblages is significantly greater, implying that the variation in extent of cohesion, as noted above between shola and monoculture plantations, for instance, is of real ecological significance. We also carried out one further check, namely, deleting bird species which occur on only one or two transects. It turns out that the computed hospitality values do not differ significantly from those computed by retaining the whole species set.

Unlike species diversity or evenness, hospitality has no meaning as a property of single assemblages. Instead

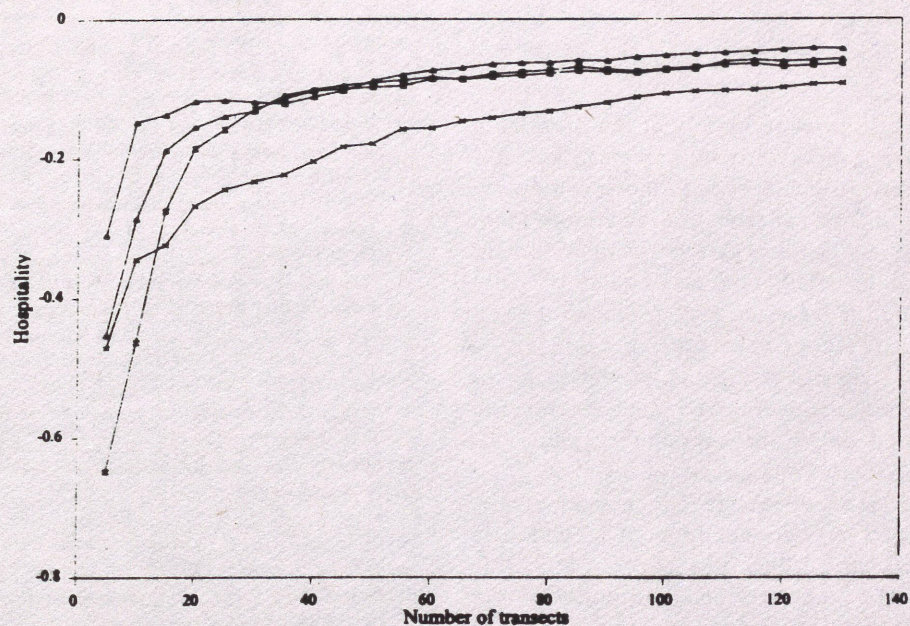


Figure 3. Hospitality as a function of number of total transects considered for four different transects selected at random.

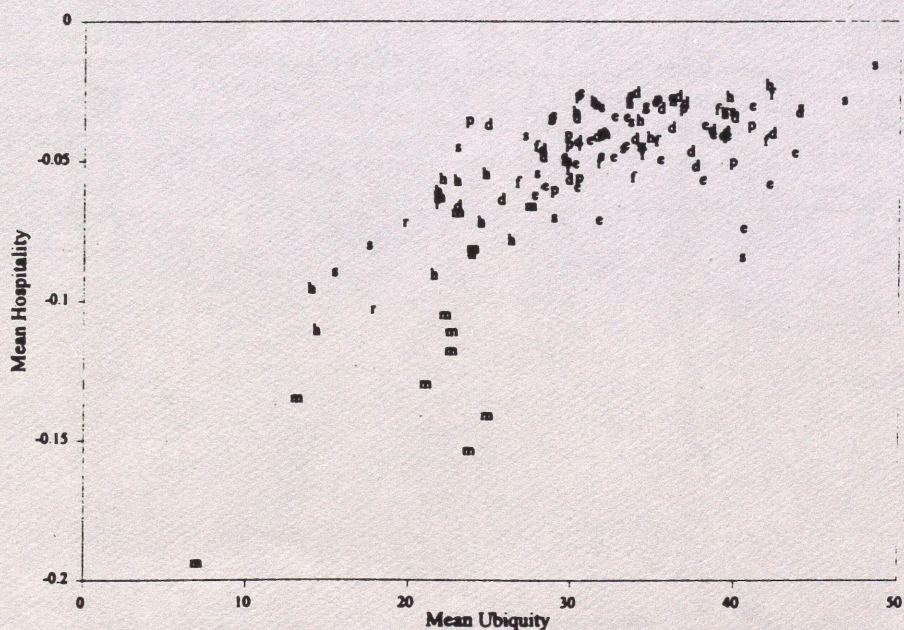


Figure 4. Mean hospitality as a function of mean ubiquity. Labels as in Table 1.

it depends on the distribution of bird species over a number of assemblages. It is then necessary to check the minimum number of assemblages for which the value of hospitality stabilizes. To do so we can compute mean hospitality for different numbers of assemblages for assemblages drawn randomly from the pool of observed assemblages. Figure 3 looks at this behaviour and suggests that the value of hospitality quickly rises up to 15 transects and reaches an asymptote around 50 transects. With a sample of 132 assemblages, we are well above this limit.

### Range and cohesion

Finally we look a little more closely at the correlation noted above between mean ubiquity and mean hospitality. In other words, assemblages with more widespread species tend to be less cohesive, and therefore more hospitable. Figure 4 illustrates this fairly tight correlation between mean hospitality and mean ubiquity. However, the correlation is by no means perfect, so that the concept of hospitality does have some additional content. The lack of tightness is especially evident at the left hand end of low ubiquity. Here there are several transects lying well below the overall regression. All these transects belong to shola forests.

These outlying shola transects are geographically rather restricted being derived from two localities namely, Eravikulam and Upper Bhavani. It is possible that the low levels of ubiquity and hospitality of the shola assemblages may be a simple consequence of the restricted geographical range of this habitat type. To assess this possibility, we recomputed the ubiquity and hospitality levels for three other habitat types, namely, evergreen, deciduous and gardens by selecting in each case a smaller subset of transects derived from a similarly restricted geographical area within one degree of latitude. In none of these cases is there a lowering of

ubiquity or hospitality levels of these other three habitat type to the levels displayed by sholas.

We may then conclude that the geographically restricted bird assemblages of montane shola/grassland complexes are significantly cohesive. This is presumably related to the fact that this high altitude habitat has a distinctive macroclimatic regime to which a limited number of species have adapted and perhaps coevolved over a long evolutionary time. These rather special assemblages of bird species evidently merit attention as a focus of conservation effort.

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## Evaluating bird communities of Western Ghats to plan for a biodiversity friendly development

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Reconciling development with conservation of biological diversity has emerged as a significant concern in recent years. This has been primarily attempted through establishment of protected areas taken out of mainstream development, and through regulating impacts of major development projects with the help of environmental impact assessment exercises. We believe that these two instruments need to be complemented by continually providing inputs into the biodiversity implications of ongoing development processes (and accompanying habitat transformations) at the landscape and regional level. It is desirable that such assessment of biodiversity implications is based on a transparent, objective methodology which could be used by a wide range of practitioners working with the emerging decentralized processes of development planning. In this paper we outline such a methodology focussing on birds. This involves assigning a conservation value to bird species based on readily available information on their geographical range, habitat preference, endangerment and taxonomic distinctiveness. This may then be translated into a mean composite conservation value for bird assemblages characteristic of different habitat types. By combining this information with that on ongoing processes of habitat transformations, we can provide an assessment of how development processes are affecting biodiversity values. We illustrate this methodology by assessing the conservation value of 586 bird species of Western Ghats, and a sample of bird assemblages of seven major habitat types of the region. We conclude that the most serious loss of biodiversity value arises in the transformation of montane evergreen shola forests/high altitude grasslands into monoculture plantations.

PLANNING for environmentally sound and biodiversity friendly development has in recent years emerged as an important concern. Minimizing the loss of biodiversity is one of the key objectives in planning for such sustainable development<sup>1,2</sup>. Conservation or protection of biodiversity is critically dependent on the kinds of habitat transformations that are ongoing in any area. The habitat transformations, in turn, depend on land use and hence are intimately connected to the overall development<sup>3</sup>.

Therefore we cannot consider conservation and development as two watertight compartments. Till now the efforts to reconcile them have primarily taken two forms; creation of additional protected areas taken out of the mainstream of development and assertion of control over the way major development projects are executed on the basis of environmental impact assessment exercises<sup>4</sup>. Both these approaches have led to positive gains, yet both have their own limitations. The protected areas approach is particularly appropriate when the focus of conservation is on one or more flagship species like the tiger or the Siberian crane. But it is inadequate when the focus shifts to conservation of the entire spectrum of diversity of life, including genetic diversity. Thus many elements of conservation interest, such as wild relatives of cultivated plants like yams occur in highly disturbed habitats such as road verges; others occur as weeds in field; yet others are restricted to climax communities such as wet evergreen forests. Multiple populations of the entire diversity of these wild relatives of cultivated plants can then only be conserved through prudent management of a whole variety of habitat types, both within and outside protected areas<sup>5</sup>. The environmental impact assessment exercises too are inadequate in their approach as well as in practice<sup>4,6</sup>. They are invoked only in case of major development projects like dams, and leave out of consideration most continual, smaller scale changes. Their treatment of biodiversity is very superficial, often limited to partial listing of major species of larger wildlife or migratory birds. They do not incorporate a proper method to assess the biodiversity loss due to landscape transformations. The environmental impact assessment procedures currently prevalent in India provide no scope for public participations<sup>7</sup>. They are also conducted as one time exercises and do not involve continual monitoring. Given these various limitations in the end they have only a limited positive impact<sup>1</sup>. Apart from the knowledge of environmental impact of major developmental projects, the impact of various kinds of land use practices on biodiversity is necessary to initiate an ecologically prudent management of natural resources. For such broad-based developmental planning, we need inputs and instruments

additional to networks of protected areas and one time environmental impact assessments.

To be effective, such inputs to development planning must deal with all of the country's landscape and waterscape and be continual since the processes of erosion of biodiversity are going on everywhere all the time. Such broad-based monitoring of biodiversity cannot be the sole responsibility of any one centralized agency; after all the ratio of scientists in the Botanical and Zoological Surveys of India to the land area of the country is 1:1 million hectares. It should instead be organized as a decentralized effort involving local organizations such as educational institutions and NGOs familiar and concerned with their own localities. Such a large scale effort will have to focus on a subset of living organisms that represent the entire taxonomic diversity and inhabit the whole range of habitats, yet are easily accessible and can be identified with some reliability. Such a subset could, for instance, comprise relatively better documented groups like birds, butterflies, ants, dragonflies, earthworms, crabs, leeches, fish, mushrooms, lichens and flowering plants. The levels of diversity in some such set of taxonomic groups should then be monitored in the full range of ecosystems or habitat types of any region; as an ongoing exercise, preferably on an annual basis.

This would generate a wealth of valuable data relevant for detailed planning of ecological management of particular ecosystems. But development planning has to proceed at a hierarchy of levels involving larger and larger spatial scales. The detailed locality specific information therefore needs to be summarized properly to provide effective inputs at higher levels. Such a process would necessarily lead to loss of some information; any priorities set on the basis of such abstraction could be open to question in specific instances. Ecologists therefore hesitate to accept such abstractions. But it is clear that development processes will go on, modifying ecosystems, further eroding biodiversity, and the best option before ecologists is to provide as much information as possible at the appropriate levels to try and influence these processes onto a biodiversity friendly course. Since information must be digested before it reaches higher levels, we must work out ways of doing so most effectively. This paper suggests one possible methodology for summarizing information generated through biodiversity monitoring as a possible input to the process of development planning<sup>3</sup>. The proposal of course, has a number of weaknesses. It is nevertheless presented here in the hope that it would stimulate debate and catalyse further progress.

Development interventions primarily affect biodiversity through transformations of habitats. Thus while direct overharvests for forest-based industry have led to local elimination of a few species, such as *Dipterocar-*

*pus indicus* in demand for manufacture of plywood, the indirect impacts such as through large scale clear felling of evergreen forests for raising eucalyptus plantations or planting of wattle on high altitude grasslands are likely to be of greater significance<sup>8</sup>. It is also far more feasible to keep track of transformations at the habitat level, especially given the availability of satellite imagery and information management systems like Geographical Information System (GIS) than to keep track of changes in populations of tens of thousands of biological species. It is therefore most efficient to organize monitoring biodiversity as a two-step process of monitoring habitat transformations and evaluating different forms of habitat transformations in terms of their implications for biodiversity<sup>9</sup>. Such a programme involves arriving at (1) a system of classification of habitat types, (2) monitoring ongoing transformations in habitat types, (3) censusing different types of habitats in terms of the elements of biodiversity that they harbour, (4) assigning values to these elements of biodiversity and (5) assessing habitat transformations in terms of how they affect biodiversity values. The final, and the most difficult step is of course (6) ensuring that information is given appropriate weightage in arriving at and implementing development priorities.

We are a part of a network, the Western Ghats Biodiversity (WGBN) that is engaged in a co-operative research programme that aims at developing and putting into practice such a methodology<sup>10</sup>. In this paper we wish to present a case study to illustrate steps (4) and (5) of this methodology namely evaluating elements of biodiversity and assessing habitat transformations in terms of how they affect biodiversity values. We will, however, supplement this discussion with some material relating to the other steps in this methodology. Their fuller details are being published elsewhere.

### Background of the study

Our case study is situated in the hill chain of Western Ghats, running parallel to the west coast of India for over 1600 km from 8°N to 21°N latitude. In width the hill chain averages 100 km; its highest peaks are around 1500 m to the north and 2600 m in the south. The rainfall ranges from 3000 mm on the coast to 7500 mm on the crestline, declining rapidly to the east. The Western Ghats constitute a substantial tract of tropical humid vegetation separated by over 1800 km from the larger contiguous tract of humid forest of Eastern Himalayas and Southeast Asia<sup>11</sup>. In consequence this tract of high levels of diversity is also characterized by high levels of endemism. Originally covered by tropical wet evergreen, moist deciduous and dry deciduous forests, the vegetation of Western Ghats has been profoundly modified through human interventions, so that it is now an intricate mosaic of various degradation stages of the

natural forest types along with plantations of rubber, eucalyptus, wattle, casuarina, betelnut, fields of paddy and gardens associated with habitation.

WGBN has initiated studies of the landscape of the Western Ghats, the distribution of biodiversity over this landscape and the ongoing transformations of the landscape in 20 localities spanning the entire geographical spread of the hill chain<sup>10</sup>. An area of about 25 km<sup>2</sup> has been mapped in each of these localities with reference to habitats defined in terms of vegetation structure and composition as discernible on spatial scales of a hectare or more. We distinguish 45 habitat or landscape element types<sup>9</sup> over the 20 localities; each locality has between 8 to 15 of these. The local people are very familiar with how this landscape has been changing over the last 10 to 20 years, what kinds of landscape elements are being transformed into what other kinds and what social and, economic forces are driving these changes. We thus have accounts of ongoing landscape transformations for all localities based on oral history as well as official documents and maps. We have also surveyed to varying degree of completeness occurrences of species of birds, flowering plants, butterflies, freshwater molluscs, freshwater insects, freshwater fishes and caecilians in representative samples of elements of various habitat types in all the localities. Of these, the bird surveys are relatively complete and constitute the basis of this case study. A companion paper<sup>12</sup> in this issue provides further details.

### Habitat transformations

For the purpose of this case study we have aggregated some of the landscape element types into fewer categories, for instance merging secondary scrub and tree savanna derived from degradation of evergreen forest as also a variety of tree monocultures such as rubber, eucalyptus, wattle and betelnut. Using the resultant seven categories, Table 1 summarizes the broad picture

**Table 1.** A schematic summary of ongoing changes in the landscape of the Western Ghats

FROM TO	SH	EV	SE	DC	SC	MP	HB
SH	F	A	A	A	A	A	A
EV	A	F	O	R	A	A	A
SE	A	F	F	A	A	A	A
DC	A	O	O	F	R	R	A
SC	O	O	F	O	F	R	A
MP	O	O	O	O	F	F	A
HB	R	O	O	O	O	R	F

F, Frequent; O, Occasional; R, Rare; A, Absent; SH, Shola/grassland; EV, Evergreen forest; SE, Semievergreen forest; DC, Deciduous forest; SC, Scrub/savanna; MP, Monoculture plantation; HB, Gardens around habitation.

of ongoing transformations of the landscape in 15 of 20 study localities. The seven habitat types are arranged roughly in order of departure from primary, natural to more and more human impacted types. The most evident tendency is for maintenance of the same type so that the diagonal elements are all shown as 'frequent' in Table 1. The only other frequent element is the conversion of scrub into monoculture tree plantations of species like *Acacia auriculiformes*. The elements above the diagonal indicate progression back to more natural types; these are largely absent or rare. The elements below the diagonal indicate conversions to more human impacted or fully managed types, these occur at a greater rate.

A variety of development interventions lead to these transformations and our objective is to appraise them in terms of biodiversity values. As argued above, such appraisal may with profit be organized as a decentralized, participatory exercise. Birds, being attractive and readily identifiable down to species are in many ways amongst the most suitable groups of organisms for this purpose. They are, however, highly mobile and therefore more likely to use a wider range of habitats and often disperse into less preferred habitats from neighbouring more preferred ones. Bird communities are therefore likely to be less sensitive to habitat changes and should not be used as the only basis of appraising the implications of habitat transformations for biodiversity values. Nevertheless, they are an appropriate choice as one of the components of such an exercise.

The next step in evaluating implications of habitat transformations is identification of the bird species pools characteristic of different habitat types. We have attempted to do so on the basis of 132 one hour transects distributed over the seven major aggregated habitat types of the Western Ghats<sup>12</sup>. A total of 212 species were encountered in the course of these transects. These do not provide information on the total species pools, but are only samples of the pools from each habitat type. Nevertheless these are a reasonable starting point for our further analysis.

### Valuing bird taxa

We need to evaluate the bird species pools characterizing the various habitat types. This is best based on an evaluation of the individual member species of the pool. This would be an exercise of quantifying the effort that the society might be willing to devote to ensure continued persistence of any given species. This would depend on a variety of attributes of the species. They belong to three major categories: rarity, extent of threat of extinction and utility<sup>13</sup>. In general, rarer the species, the more threatened the species, the greater the utility of the species, the greater the effort that would be merited to ensure its continued persistence.

We may then assign to any particular species a conservation value reflecting this effort, such that the value would increase with rarity, extent of threat and utility. The actual values could either be ranks along a scale or a specific number. We propose to leave out attempts to quantify utility of bird species and assign quantitative values ranging between 0 and 1 on the basis of 7 attributes relating to rarity and extent of threat. Four of these values relate to the geographical range: G1, over the entire world divided into 6 zoogeographic regions; G2, over the oriental region divided into 9 subregions; G3, over the Indian subregion divided into 8 provinces; and G4, over the Malabar (Western Ghats plus West coast) province divided into 4 sections. The conservation value for a taxon by geographic range is given as:

$$G = (N - a)/(N - 1),$$

where  $N$  is the number of subdivisions at a given level and  $a$  is the number of subdivisions from which the taxon is known. This ensures that the more restricted the range on any of these scales, the greater would the conservation value be. The conservation value of each taxon by habitat preference was computed as

$$H = (N - a)/(N - 1),$$

where  $N$  is the total number of bird habitat types over the Western Ghats region and  $a$  the number of habitats favoured by a given taxon. This ensures that the more limited the habitat range of a species, the greater would the value be. The conservation value of a taxon reflecting its taxonomic distinctness was calculated as:

$$T = 1/(a \times b),$$

where  $a$  is the number of species known in the family to which the taxon belongs and  $b$  is the number of races under the species. Rarity is thus sought to be captured in terms of narrowness of geographical range, narrowness of habitat preference and limitations on number of related taxa. The conservation value by degree of endangerment was assigned as

$$E = p,$$

where  $p$  is the proportion of endangered taxa in the family to which the taxon belongs. This methodology has been discussed earlier in some detail by Daniels *et al.*<sup>14</sup>

Admittedly these attempts to capture rarity and endangerment in terms of broad patterns of geographical distribution, habitat preferences, taxonomic position and number of related taxa recorded as threatened are crude. Nevertheless they are based on information which is available for all bird species of Western Ghats, indeed of the whole country, and therefore permit an evaluation exercise which is reasonably objective and accessible for verification by all who may be interested<sup>15-17</sup>. This

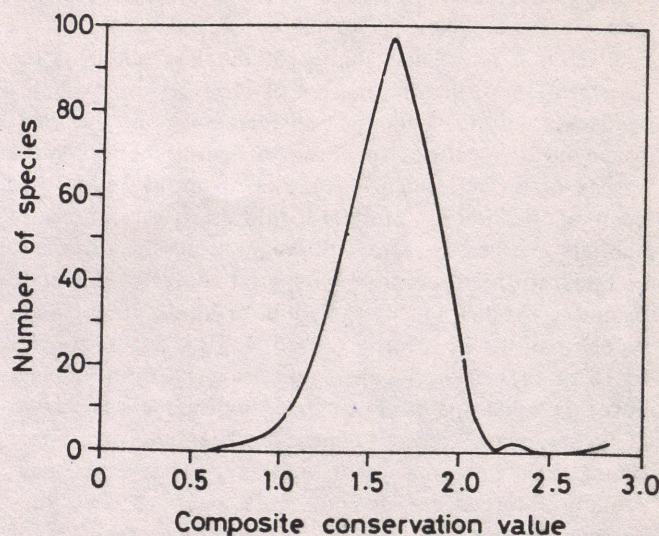


Figure 1. Distribution of composite conservation value in 586 species of birds in Western Ghats.

overcomes problems which plague other more subjective exercises, including the listing of threatened species in IUCN sponsored red data books. Thus the peafowl (*Pavo cristatus*), the Nilgiri wood pigeon (*Columba eliphinstonii*), lesser adjutant stork (*Leptoptilos javanicus*) and the redfaced malkoha (*Phaenicophaeus pyrrocephalus*) are the 4 Western Ghats species included in the list of endangered species<sup>17</sup>. However, of these four, the peafowl is widely distributed in India with many pockets of local abundance thanks to religious beliefs and the lesser adjutant stork is locally quite common in its appropriate habitat.

### Distribution of conservation values

The 212 species encountered by us over the 132 transects are a subset of the 586 species of the Western Ghats<sup>18</sup>. We have computed for the set of 586 species of Western Ghats conservation values for each of these 7 parameters, and a composite conservation value (CCV) as the sum of four values, namely the mean of the four values derived from geographical distribution and the other three values related to habitat preference, taxonomic uniqueness and degree of endangerment. As Figure 1 shows, the CCV ranges between 0.66 for the Indian jungle crow, widespread, habitat generalist, a member of a speciose family with many races and of a family in little danger of extinction to 2.77 for crab plover, a wader with a restricted geographical distribution, narrow habitat preferences, and the only species in the family Dromadidae. The cumulative frequency distribution rises rapidly at either end, between 0.66 and 1.11 and between 1.94 and 2.77, with about 520 species

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**Table 2.** Conservation values of 28 selected species of birds from 586 species of Western Ghats

HB No	Species	Rank	CCV	G1	G2	G3	G4	H	T	E
1063	Grey hypocolius	2	2.28	0.80	0.00	1.00	1.00	1.00	0.33	0.00
260	Rock bush quail	4	2.08	1.00	1.00	0.85	1.00	1.00	0.00	0.11
277	Red spurfowl	5	2.07	1.00	1.00	1.00	1.00	0.95	0.00	0.11
1638	Whitebellied shortwing	7	2.02	1.00	1.00	1.00	1.00	1.00	0.00	0.02
1637	Rufousbellied shortwing	7	2.02	1.00	1.00	1.00	1.00	1.00	0.00	0.02
299	Indian red junglefowl	11	1.99	1.00	1.00	0.85	1.00	0.91	0.00	0.11
599	Redfaced malkoha	12	1.99	1.00	0.87	1.00	1.00	1.00	0.01	0.01
1220	Mount Abu W.T. babbler	13	1.99	1.00	1.00	0.85	1.00	1.00	0.00	0.02
710	Trogon	14	1.98	1.00	1.00	0.85	1.00	1.00	0.01	0.01
1135	Yellowthroated bulbul	15	1.97	1.00	1.00	0.85	1.00	1.00	0.01	0.00
1756	Bourdillon's blackbird	16	1.97	0.80	1.00	1.00	1.00	1.00	0.00	0.02
853	Pygmy woodpecker	19	1.95	1.00	1.00	1.00	0.66	1.00	0.00	0.03
614	Striated scops owl	20	1.94	0.80	1.00	0.85	1.00	1.00	0.01	0.02
1874	Forest wagtail	542	1.09	0.80	0.37	0.14	0.00	0.73	0.02	0.00
135	Brahminy kite	543	1.09	0.80	0.25	0.00	0.00	0.78	0.00	0.04
953	Indian golden oriole	545	1.08	0.60	0.62	0.42	0.00	0.65	0.02	0.00
748	Bluetailed bee-eater	547	1.07	1.00	0.00	0.28	0.00	0.74	0.01	0.00
130	Crested honey buzzard	549	1.04	0.80	0.25	0.00	0.00	0.74	0.00	0.04
750	Small green bee-eater	553	1.00	0.60	0.87	0.42	0.00	0.52	0.00	0.00
209	Peregrine falcon	554	0.99	0.00	0.37	0.00	0.00	0.87	0.00	0.03
124	Blackwinged kite	555	0.99	0.40	0.12	0.14	0.00	0.78	0.00	0.04
1884	Grey wagtail	556	0.98	0.60	0.00	0.00	0.00	0.83	0.00	0.00
1006	Indian myna	557	0.93	0.20	0.50	0.14	0.00	0.70	0.00	0.02
1407	Brown flycatcher	558	0.90	0.80	0.00	0.28	0.00	0.61	0.00	0.02
917	Eastern swallow	560	0.86	0.00	0.12	0.00	0.00	0.83	0.00	0.00
965	Indian grey drongo	561	0.85	0.80	0.75	0.42	0.00	0.35	0.00	0.00
736	W.B. kingfisher	562	0.73	0.80	0.62	0.57	0.00	0.22	0.00	0.01
1057	Indian jungle crow	563	0.66	0.80	0.87	0.71	0.00	0.04	0.00	0.02

HBNo, Reference number of species as in ref. 15.

CCV, Composite conservation value; Rank, Rank of the species according to its CCV; G1, G2, G3, G4, H, T, E as in the text.

**Table 3.** Distribution of composite conservation values in some broader groups of birds

Group of birds	Nosp	Mg	Mr	Sdg	Sdr	t-val	p-val
Hérons, egrets, bitterns	15	1.22	1.56	0.24	0.23	-5.35	0
Hawks, vultures, etc.	40	1.45	1.55	0.25	0.24	-2.48	0.01
Pheasants, partridges, and quails	14	1.72	1.54	0.23	0.24	2.61	0.01
Curlews, sandpipers, snipes and woodcocks	26	1.39	1.55	0.13	0.24	-3.28	0.00
Babblers	24	1.78	1.54	0.13	0.24	4.86	0
Thrushes and chats	29	1.66	1.55	0.20	0.25	2.46	0.01

Nosp, Number of species of the respective group; Mg, Mr, Mean CCV of the group and the rest of the birds of Western Ghats; SDg, SDr, Standard deviation of CCV of the group and the rest of birds. The *t*-test was used for detecting the statistical significance of the difference between mean values.

in the middle accounting for the values between 1.11 and 1.94. The bottom 22 and top 21 species with composite values substantially higher or lower than the majority are then of special interest. Fifteen out of these are birds of aquatic habitats, egrets, cormorants, cranes or skuas. Since our focus is on terrestrial habitats, we

may take a closer look at the other species (Table 2). The species with highest conservation value include thrushes, babblers, woodpeckers, trogon, characteristic of forest habitats with narrow ranges at least at the subspecies level; and gallinaceous birds (quails, junglefowls, etc.) that are extensively hunted and thereby threatened. The species with the lowest conservation values include passerines, swallows, hawks and falcons with a broad range of habitat tolerance and a wide geographical distribution, many of whom have adapted to human presence.

It is also of interest to examine the distribution of the composite conservation value amongst the broader groups of birds at family/subfamily level. Table 3 provides this information for six groups for which the group values are significantly lower or greater than for the rest in the pool of 586 Western Ghats species. Two groups of water birds, herons and curlews, and one group of terrestrial birds, hawks and vultures have significantly low composite conservation values. These have all very broad geographical distributions. Although the hawks and vultures have a significantly higher value in terms of endangerment, and curlews and sandpipers significantly higher value because of their more limited habitat pref-

Table 4. Composite conservation value (CCV) of habitats

Habitat	No Trans	No Birds	SD	Mean	Composite conservatin value			
					SD	Max	Min	Med
Shola/grassland	11	14.04	4.14	1.57	0.05	1.63	1.47	1.55
Evergreen forest	24	18.45	4.92	1.47	0.06	1.57	1.30	1.45
Semievergreen fores	13	18.92	4.25	1.49	0.05	1.56	1.40	1.47
Deciduous forest	23	18.95	5.32	1.44	0.05	1.58	1.32	1.44
Scrub/savanna	17	17.88	6.53	1.40	0.10	1.59	1.20	1.41
Monoculture plantation	13	13.46	5.61	1.40	0.08	1.56	1.26	1.39
Home garden	23	21.39	6.55	1.37	0.06	1.47	1.25	1.38
Paddy fields	5	19.00	4.69	1.30	0.05	1.36	1.23	1.32

erence, their CCVs are still significantly lower than the general population.

Three groups, namely thrushes and chats, pheasants and quails and babblers and laughing thrushes have significantly higher CCVs. These they owe in all three cases to more restricted geographical distributions, and in the case of pheasants and quails also to significantly higher degree of endangerment. Three other groups of birds are notable for relatively high values along some of the dimensions of conservation value, though their CCV is not significantly higher. These include ducks, geese, pigeons and doves that have significantly high values in terms of endangerment, and woodpeckers that have significantly higher values in terms of restricted geographical distribution. Virakkala *et al.*<sup>19</sup> have suggested the use of woodpeckers as indicators of the health of forest habitats of Finland. For the terrestrial habitats of Western Ghats, the babblers would evidently be an appropriate choice as the group with the highest CCV.

### Valuing habitats

Having thus quantified the conservation value at the species level, we can proceed to assign values to habitats on the basis of species they harbour. Most of the earlier exercises of this nature have primarily relied on species richness. An important advance in this context has been the use of taxonomic information as suggested by Vane Wright and his co-workers<sup>20</sup>. Our concept of mean composite conservation value is another attempt in this direction. Table 4 provides the mean composite conservation value for the eight habitat types. It is notable that the two habitat types with lowest mean CCV, gardens and scrub savanna are also richest in the number of species whereas more natural habitats like shola-grassland and evergreen forest harbour comparatively lower number of rarer species which have a high conservation importance. This is because the former habitats are highly heterogeneous spatially and are colonized by a large number of opportunistic species with wide geographical distributions and broad habitat tolerances.

It then appears appropriate not to base conservation decisions on simple species richness, strengthening the case for using a measure such as the mean composite conservation value. The mean CCV for shola-grassland is significantly higher than all other values, that of evergreen and semi-evergreen forests significantly higher than that of scrub-savanna and home gardens, and that of deciduous forests significantly higher than that of gardens (all statistically significant at  $p < 0.05$ ). The differences between evergreen forests, semi-evergreen or deciduous forests and monoculture tree plantations are not significant. A caveat is, however, in order here. All the localities surveyed by us are a highly intricate mosaic of several of these habitat types. In particular, the monoculture tree plantations surveyed are of small extent and tend to abut on patches of evergreen and deciduous forests. Their bird communities though often poorer in total number of species, are made up of many elements from neighbouring forest habitats. This may be the reason why their mean CCV is not significantly lower in comparison with evergreen and deciduous forest types.

### Appraising transformations

The next step is to combine the information on mean CCVs with that on ongoing habitat transformations and quantify their implications in terms of loss of biodiversity values. It is clear that the broad trend of transformations is from the primary, more natural types of higher mean CCV to secondary, more human impacted types of lower mean CCV. This is intuitively obvious and our analysis may be said to have added little to our understanding. However, this is not entirely so. The most frequent transformation is from scrub to tree monocultures, transformations which are often assumed to have adverse biodiversity consequences. Our analysis, however, suggests that this may not necessarily be the case; the mean CCV of monocultures is in fact slightly higher, though not significantly so. Another frequent transformation involves raising monoculture plantations in the shola-grassland systems. Forest managers argue

that this transformation in fact enhances biodiversity values as it enhances the net biomass<sup>21,22</sup>. Our analysis suggests otherwise, mean CCV for shola-grasslands being significantly higher than that for monoculture plantations.

This suggests that the analysis of the type presented here can indeed lead to non-obvious conclusions of relevance to management decisions, and therefore of value to development planning. Even if some of the other conclusions appear to be obvious, their being derived on the basis of an objective, verifiable methodology is still of value. However, we must emphasize that this is only a beginning and meant to demonstrate the significance of a possible methodology which in its present form has many undoubted shortcomings. The first most obvious shortcoming is the reliance on just one particular group of organisms – the birds. To enhance its usefulness, the analysis should be extended to as many other taxa as possible favouring different broader adaptive zones available in that area. Secondly, our analysis leaves out of consideration the relative extent of different habitat types, at the local as well as regional scales. Thus not only may shola-grasslands be of considerable value because they harbour bird species with a high mean CCV, but also because this habitat type is of very limited distribution in higher reaches of the Western Ghats. Furthermore, its ongoing fragmentation may be a matter of serious conservation concern. It is necessary to elaborate specific methodologies to include these additional considerations.

Finally the all-important question of how the insights derived from such an analysis are to be incorporated in specific management decisions such as in taking up specific plantations activities, or at a larger scale in the broader process of development planning remains open. We suggest that before any developmental projects or broader land use changes are implemented, these type of studies, both in short and long term, will help us in a more reasonable cost benefit analysis upon which to base decisions to steer development on to a more sustainable and environmentally friendly path. Hopefully we will move in this direction as a more decentralized process of development planning takes root in the country<sup>23</sup>. The fact that the methodology sketched above easily lends itself to an objective, participatory exercise should render it easier to incorporate it in such a decentralized process of planning.

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## Hierarchical Partitioning of Tree Diversity Across Spatial Scales: A Case Study from the Nilgiri Biosphere Reserve, Southern India

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### ABSTRACT

Based on the data collected from 60 strip transects (250 m × 4 m), we have investigated how the variation in different attributes of vegetation is partitioned across different spatial scales in the Nilgiri Biosphere Reserve in Southern India. Traditional ANOVA formulation is used for the variation of stem density, and of structural attributes such as the girths and heights of trees. An equivalent formulation based on Simpson's index is used for species diversity. The proportion of between-transect variance is large (about 80%) for the number of individuals per transect and for the number of species per transect. However, it has a low (10-15%) value for girths, heights and species diversity. In fact, for the last three attributes, a large proportion of variance (about 75%) is concentrated within 10 m × 4 m quadrats. We describe the extent to which our results are affected by different levels of sampling intensity, as simulated by sampling fewer transects, fewer quadrats per transect, and fewer trees (using higher girth and height cutoffs). It is seen that the estimate of between-transect variance can be reliably obtained even with a modest sampling effort (about 20 transects, each 0.1 ha in area).

*Key Words* : ANOVA, Diversity partitioning, Nilgiris, Simpson's index, Spatial scales, Species diversity, Tree diversity.

### INTRODUCTION

Late 1980s and early 1990s saw a steep increase in the studies of biodiversity across the globe (Harper and Hawksworth 1994). This was partly from an increased awareness of the imminent loss of many forms of life, engendered by a number of anthropogenic influences, and, to an extent, from the increasing realization of the commercial potential of many yet-to-be-discovered natural products. The Biodiversity convention, adopted by most countries, provided a more formal label (Inventorying and Monitoring Biodiversity) for the studies focusing on the distributions of plants, animals and other life forms

(Quarrie 1992). Consequent co-ordinated, multinational and multi-institutional efforts have led to the compilation and analysis of the patterns of distribution of many different taxa, at a large number of locations spread across the globe (see, for example, Reid and Miller 1989, Hawksworth 1995, Gaston 1996).

One can discern three (amongst many) main lines of investigations in these programs. The first one deals with the identification of regions which are exceptionally rich in biodiversity - the 'hot spots' (Meyers 1990). The second one involves developing methods for making such assessments in a systematic and quantitative manner (e.g., Daniels et al. 1991, Spellerberg 1992). The third one involves examining the factors which govern the patterns of biodiversity (Ricklefs and Schluter 1993). However, one of the aspects which has received relatively less attention, pertains to the hierarchical organization of diversity; and this is the focus of our investigations described here. For the ease of interpretation as well as of analysis, we have restricted ourselves to one taxon (trees), and a single dataset collected from a relatively small (~5500 sq. km) geographical region. The framework, however, is readily extendable to other (and more) taxa and to larger spatial scales.

Quantitative descriptions of diversity have been of two kinds. One deals with the alpha, beta and gamma diversities which describe the local diversity, species turnover, and the size of the species pool in a large region respectively (Whittaker 1972). The other deals with different types of diversity indices (Shannon Weaver index, Simpson index, etc.), which attempt to summarize the information on the number of species together with that on their abundances in a single number (e.g., Pielou 1975, Ludwig and Reynolds 1988). Recently, Lande (1996) critically reviewed both of these approaches, and has suggested how they can be brought under a common framework. In particular, he has drawn attention to the fact that Simpson's index can be expressed as a variance, and has indicated how this can be used, under the ANOVA framework, for expressing alpha- and beta-diversity indices in a more logical manner. More importantly, this framework, commonly employed in studies on human genetic diversity (e.g., Nei 1987, Barbujani et al. 1997), enables one to partition the diversity (i.e., variance) among different hierarchical levels.

In the present study, we describe how the tree species diversity is partitioned across several different levels - between habitats, between transects, within quadrats in a transect and within subquadrats in a quadrat. We also investigate the partitioning of variance of other attributes such as density (number of individuals per unit area), girths and heights of trees. The sensitivity of the results to varying levels of sampling intensity has also been examined.

## STUDY AREA

The survey was conducted in the Nilgiri Biosphere Reserve (NBR), a region approximately 5520 sq. km in area, located between 10° 50' and 12° 16' N Latitude and 76° 0' and 77° 15' E Longitude. The Nilgiri hills, an offshoot of the Western Ghats forms the central part of the NBR. This mountain mass with an elevation ranging from 1800 m to 2400 m forms the core of the biosphere (Hockings 1989). It is bounded in the north by the Mysore plateau (part of Deccan plateau) with an elevation of 800 m to 1000 m,

in the east and south by the Coimbatore plains (elevation of 300 m to 400 m) and in the west by the narrow strip Malabar plains (elevation of 150 m) leading to Arabian sea.

The topographical diversity of the Nilgiris has led to a great diversity of temperature and rainfall (Lengerke 1977). The mean annual temperature varies with the altitude: about 26° below 500 m, around 23° in the 500-1000 m range, and below 20° at higher altitudes. On the higher elevations there is incidence of frost wherein minimum temperature can reach as low as 0°C. The Western part of the biosphere receives over 4000 mm rainfall and the Easternmost part, as low as 500 mm. There is thus a distinct rainfall gradient across West-East directions which has played a crucial role in determining the vegetation of the biosphere reserve.

Being located in the two biogeographical provinces of India (Malabar rain forest and Deccan thorn forest), NBR encompasses a spectrum of vegetation types. The topographical and climatic diversity of the biosphere reserve has resulted in lush rainforests on the western side and dry thorn forest on the east through a deciduous forest belt. Major types of forest vegetation found in NBR are: (a) Tropical evergreen forest type, (b) Tropical moist deciduous forest type, (c) Tropical dry deciduous forest type and (d) Tropical dry thorn forest type. Additionally, along the water courses, Riverine or gallery forest, a different vegetation type identifiable by its assemblage of characteristic species is also present. On the higher reaches of the mountains there is a characteristic association of two climax vegetation existing in equilibrium namely Shola (tropical montane stunted evergreen) and grassland. A more detailed description of the vegetation is available in Champion and Seth (1968) and Prabhakar (1994).

## METHODS

The survey was carried out by two of us (HSS and RP) at different time points between 1990-1996. Based on a detailed map of the NBR, 60 sites were chosen so as to cover the region in a relatively uniform manner. Moreover, an adequate representation of the six major habitat types in NBR (riverine, evergreen, shola, moist deciduous, dry deciduous and scrub) were also ensured. At each location, a 250 m long and 4 m wide transect (Gentry 1988) was laid, and divided lengthwise into five quadrats, 50 m in length. Each quadrat was further divided into five 10m long subquadrats. All stems above 10 cm in girth encountered in a subquadrat were enumerated, i.e., the species identity, GBH (circumference to the nearest 0.5 cm, at 1.3 m from the ground) and height (to nearest 0.5 m) was recorded. Heights upto 6 m were measured using a calibrated rod, while visual estimation was used for taller trees. Multiple stems belonging to the same tree were separately recorded if they exceeded 10 cm in girth; however, only the largest stem of the multi-stemmed tree was included in the subsequent analysis. In all such cases, the stem with largest GBH was also the tallest one.

## Data Analysis

We use the distance-based ANOVA framework, as described by Excoffier et al. (1992) and Lande (1996). If  $X_1, X_2, \dots, X_N$  represent a sample of  $N$  values, then it can be easily seen that

$$\frac{1}{2N^2} \sum_{i=1}^N \sum_{k=1}^N (X_i - X_k)^2$$

is the variance of  $X$ . We can interpret  $(X_i - X_k)^2$  as the squared Euclidean 'distance' between two observations  $i$  and  $k$ .

If a dataset consists of  $M$  species, we represent each individual tree as a point in an  $M$  dimensional space i.e., as a vector  $(Y_1, Y_2, Y_3, \dots, Y_M)$ . For an individual belonging to the  $j$ th species, we define  $Y_j = 1$  and  $Y_q = 0$  for all  $q \neq j$ . This ensures that the squared distance between any two individuals is  $= 0$  if they belong to the same species, and  $= 2$  if they belong to different species.

If  $N_1, N_2, \dots, N_M$  represent the number of individuals of the  $M$  species, and  $p_1, p_2, \dots, p_M$  their proportions in the data, the sum of squared Euclidean distances between all pairs of individuals in this dataset, divided by  $2N^2$ , can be seen to be equal to

$$\frac{1}{2N^2} \sum_{i=1}^M 2N_i(N - N_i)$$

which is equal to

$$\sum_{i=1}^M \pi_i(1 - \pi_i)$$

which in fact is equal to  $S$ , Simpson's diversity index of this community.

We note that by using the technique of Principal Component Analysis for the  $N \times M$  data matrix described above, we can obtain a set of (new)  $M$  uncorrelated axes (variables), related to the old set of axes by an orthogonal transformation (rotation). The total variance of the dataset would be the sum of the variances for all the  $M$  (uncorrelated) variables. The value of the total variance so obtained would be identical to the one obtained from the sum of squared Euclidean distances, since the distances are invariant under an orthogonal transformation. Furthermore, as shown above, the value of the variance is equal to the value of Simpson's index of diversity. We can therefore use Simpson's index to compute the partitioning of diversity between different hierarchical levels as in the standard ANOVA formulation (e.g., Sokal and Rohlf 1995).

We have consistently used Lande's procedure for estimating the between-groups variance. However, as discussed below, this procedure does involve a slight departure from the traditional ANOVA approach. We therefore repeated some of our computations using ANOVA. The differences between the two sets of values were found to be negligibly small for our dataset.

### Simulation

To estimate the sensitivity of our results to the intensity of sampling, we have adopted the subsampling approach. In the transect-based simulations, we randomly selected  $n$  transects, and obtained estimates for the between-transect proportion of variance. This computation was carried out for values of  $n$  ranging from 2 to 58, with 100 replicates for each value of  $n$ . The same procedure was repeated by randomly selecting 2 to 299 quadrats and separately by selecting 2 to 1499 subquadrats.

In another approach, we used all the transects, but selected  $k$  contiguous subquadrats from each of the transects. Simulations (100 replicates) were carried out for different

values of  $k$  ranging from 1 to 24, corresponding to sampling intensities of 4%, 8%, ..., 96%. In each instance, we computed the values of Simpson's index at the different spatial scales (sampling units) and the corresponding proportions of variance of diversity partitioned across these scales. We have also repeated the above simulations using (instead of all 60) a smaller number of transects (ranging from 5 to 45), with 100 replicates for each case.

In yet another approach, we varied the girth cut-off, i.e., considered only those trees whose GBH was greater than 'g', where 'g' was varied from 20 cm to 100 cm in steps of 10 cm. We also repeated our calculations by using different height cut-offs, from 2 m to 15 m in steps of 1 m.

## RESULTS

The dataset of 60 transects included 5373 individuals belonging to 364 species, inclusive of only one unidentified species. The most abundant species is *Anogeissus latifolia* (219 individuals, accounting for 4.07% of the total), followed by *Lasianthus venulosus* (169, 3.14%). The 12 most abundant species (3.3% of the species) together contribute 26% of the individuals while the top 37 (20.2%), for about 50% of the individuals. A total of 84 species (23%), on the other hand, are represented by only a single individual, and the least abundant 50% of the species, represented by five or fewer individuals, account for just 0.1% of the total number of trees in the data. Summary statistics on the stem density, number of species and species diversity at the transect, quadrat and subquadrat level are reported in Table 1.

The maximum girth seen in the data was 665 cm for a *Ficus tsjakela* tree, followed by 620 cm for *Ficus arnottiana* and 564 cm for *Mangifera indica*. The mean, median and standard deviation of girths were 48.6, 30.0 and 51.2 cm respectively. The maximum height was about 35 m, recorded for several different species such as *Poeciloneuron indicum*, *Ficus arnottiana*, *Ficus benghalensis*, *Calophyllum apetalum* and *Paluquium ellipticum*. The mean, median and standard deviation of heights were 9.4, 8 and 5.5 m respectively.

There were expectedly substantial differences between habitats for tree density, species richness and diversity with high values for evergreen and shola (the montane high altitude patches) and low values for scrub and dry deciduous types. However, since the sample size (number of transects in each habitat) was not large, quantitative comparisons of these differences has not been undertaken in the present instance.

### Partitioning of Species Diversity

The value of Simpson's index for the entire dataset is 0.9894. For the 60 transects, the value of Simpson's index ranges from 0.4694 to 0.9619, with a weighted mean of 0.8842. From these two values, the proportion of between-transect variance of species diversity is seen to be 10.63%. In other words, about 90% of the variance of species diversity is found within transects.

Along similar lines, we have computed, for each transect, the relative proportions of between-quadrats and within-quadrats variance of species diversity. The between-quadrat proportion ranged from 2.7% to 29.3%, with a mean of 9.8% and median of 8%.

Table 1. Summary Statistics for the distribution of trees at the transect, quadrat, and subquadrat levels. The areas of these units were 0.1 ha, 0.02 ha and 0.004 ha respectively. Since the focus of the present analysis is on Simpson's index of diversity, empty quadrats (4/300) and empty subquadrats (225/1500) have been excluded for the computation of summary statistics.

	Transects (n = 60)	Quadrats (n = 296)	Subquadrats (n = 1275)
No. of Individuals			
Mean	89.6	18.2	4.2
S.D.	66.4	14.5	3.5
Minimum	16	2	1
Median	62	13	3
Maximum	283	80	25
No. of Species			
Mean	21.8	8.8	3.2
S.D.	11.2	5.6	2.2
Minimum	8	1	1
Median	19	7	2
Maximum	53	32	17
Simpson's index			
Mean	0.862	0.768	0.481
S.D.	0.081	0.136	0.307
Minimum	0.469	0	0
Median	0.875	0.800	0.500
Maximum	0.962	0.950	0.935

Finally, we have estimated the proportion of variance partitioned across the four hierarchical levels. We find the between-habitat proportion to be 3.2%, between-transects-within-habitats to be 7.4%, between-quadrats-within-transects to be 6.0%, between-subquadrats-within-quadrats to be 17.5% and within-subquadrats to be 65.9%. Thus, a very large proportion of variance in species diversity seems to be concentrated in the small spatial scale of a subquadrat.

### Variance Partitioning of Other Attributes

It would be worthwhile to consider how the variance of other attributes is partitioned among different spatial scales. As explained in the methods, we have used the standard ANOVA design for these computations.

For the tree density, within-transect proportion was 21.3%, and between-transect 78.7 percent. Similarly, for species density (number of species per unit area), the within-transect component amounts to 18.7%, and between-transect to 81.3 percent.

For tree heights, on the other hand, the within-transect variance was about 87%, a large proportion of which (83% of the total) was within-quadrats. A similar pattern is seen

for girths. The within-transect component amounts to 84.4%, a large proportion (79.7% of the total) being the within-quadrats component of variance.

### Sensitivity to Sampling Intensity

The estimated value of between-transect variance (Figure 1a) shows a rapid initial increase, followed by a plateau. This pattern persists more clearly in the log-log plot (Figure 1b), where saturation seems to have been reached around the sample size of 20 transects. Thus, estimates obtained from about 20 transects seem to differ very little from those from the full dataset. The value of between-transects diversity thus seems to be relatively insensitive to the sample size (once it is adequately large), as judged by the number of transects. This conclusion is strengthened by the results of our simulations wherein we had sampled a smaller area per transect. Even when 5, 10 or 20 contiguous subquadrats are used per transect, the log-log plot of between-transect variance vs number of transects seems to attain a constant value by the time the number of transects reaches about 20.

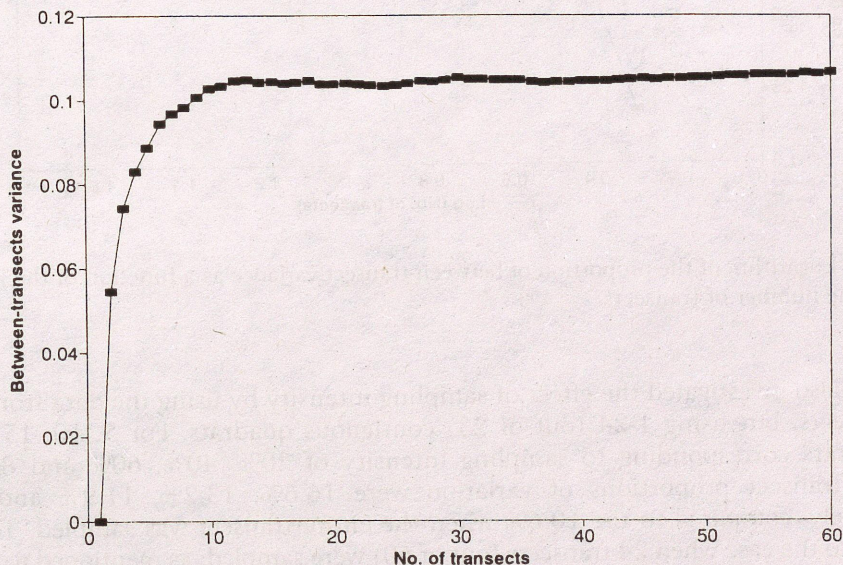


Figure 1a. The proportion of between-transect variance as a function of the number of transects.

As mentioned in the Methods section, we have also attempted to simulate the effect of sampling intensity by randomly selecting quadrats and subquadrats. For a constant sampled area (e.g., a one hectare area sampled by choosing 10 out of 60 transects, 50 out of 300 quadrats or 250 out of 1500 subquadrats) the number of species is seen to increase as the area of the sampling unit decreases. Thus, a subquadrat-based sampling records more species than the quadrat-based one, which in turn records more species than the

transect-based sampling (data not shown). However, the values of Simpson's index of diversity obtained by the three methods are nearly the same; there was no uniform, consistent pattern among the magnitudes of Simpson's index when similar total areas were samples by the three approaches.

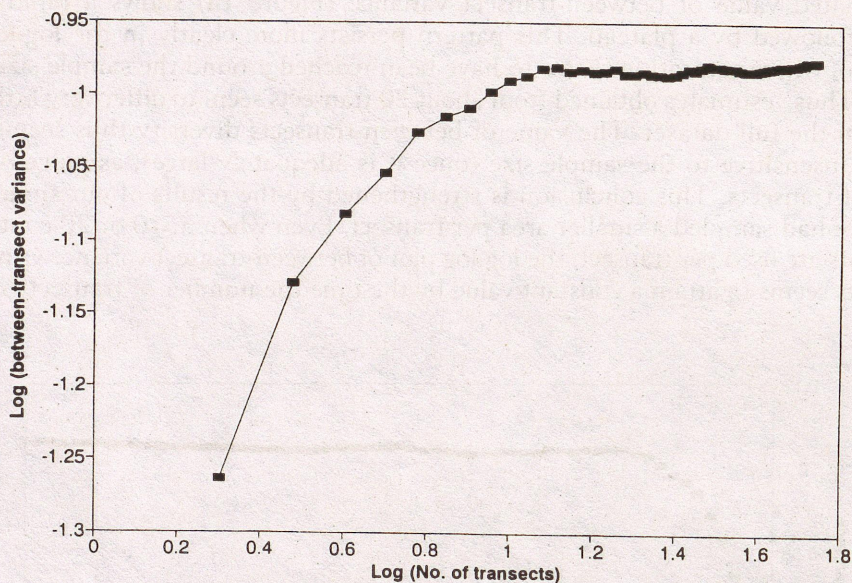


Figure 1b. Logarithm of the proportion of between-transect variance as a function of the logarithm of the number of transects.

We also investigated the effect of sampling intensity by using the data from all the 60 transects, but using 1-24 (out of 25) contiguous quadrats. For 5, 10, 15 and 20 subquadrats corresponding to sampling intensity of 20%, 40%, 60% and 80%, the between-transect proportions of variation were 16.6%, 13.2%, 11.9% and 11.2% respectively, compared to the 10.6% when the entire transect was sampled. This is in contrast to the case when 24 transects (out of 60) were sampled; as mentioned earlier, the estimated value stabilizes around 10.6% by the time about 20 transects are sampled. In other words, subsampling for example 40% of the transects leads to a slightly lower estimate of the between-transect variance than that obtained from subsampling 40% area of all the transects.

There is also a small but discernible difference between the results obtained by sampling contiguous versus non-contiguous areas within individual transects. Thus, the between-transect proportion of variance is 13.2% when two full quadrats (all five subquadrats in each) are sampled per transect. However, it reduces to 11.4% when all the five quadrats are chosen per transect, but only two subquadrats from each quadrat. This pattern is consistently seen for the different combinations of quadrats and subquadrats; for a constant area per transect, contiguous sampling leads to a higher value of between-transect variance than non-contiguous sampling within a transect.

### Comparison with a Random Pattern

The values obtained above can be more meaningful if compared to those obtained from other datasets, either from a different region, or for other taxonomic groups. We can, however, attempt to obtain some measure of the magnitude of spatial autocorrelations in the patterns of the distribution of trees using a randomization approach. In other words, we ask the following question: If the species were to be distributed randomly, while preserving the number of individuals in each subquadrats, and the overall number of each species, what would have been the effect on the partition of the variance of species diversity? Results obtained from 200 simulations show that the among-transect variance reduces to 1.1% from 10.6%, while the within-subquadrats component increases from 66% to about 75%. Thus, randomization effectively eliminates the among-transects component, while the within-subquadrats component shows only a modest increase. This seems to point to a noticeable segregation of species across transects, most probably attributable to the existence of the different habitat types, ranging from the wet riverine to the dry scrub.

### Effect of Varying Girth and Height Cut-offs

We have examined the effect of sampling a smaller number of individuals by using a higher girth cut-off. By gradually increasing the value from 10 cm to 100 cm, the number of individuals comes down from over 5000 to below 1000. The value of Simpson's index,

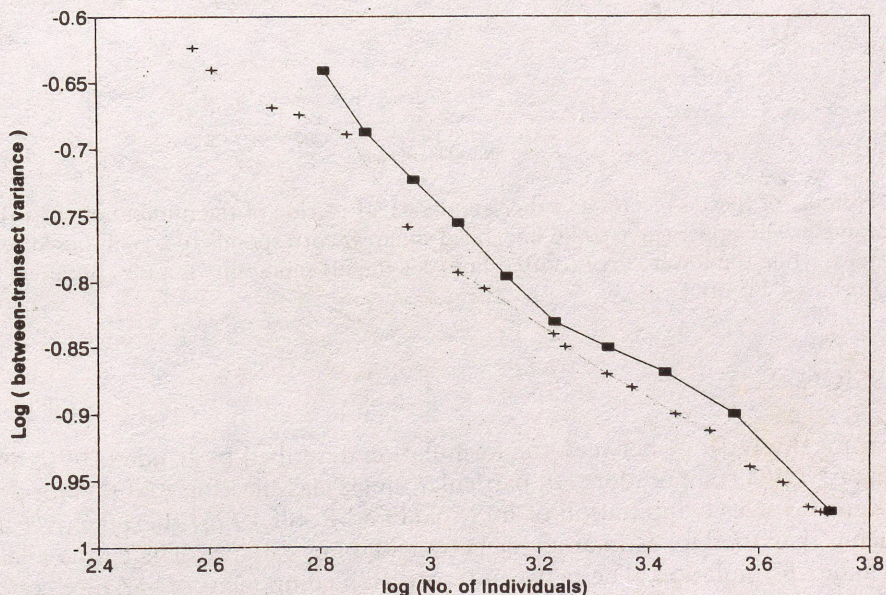


Figure 2. Logarithm of the proportion of between-transect variance as a function of the logarithm of the number of individuals sampled. The upper curve (solid line, filled squares) corresponds to a girth-based selection of trees, while the lower curve (dotted line, + symbol) represents samples obtained from a height-based cut-off.

however, shows only a marginal decrease (less than 1%) despite the almost five-fold reduction in the total sample size. A similar result holds good when different height cut-offs were used. However, the proportion of between-transect variance seems to increase rather rapidly as the sample size decreases (Figure 2). The corresponding log-log plots shows a near-linear behaviour, indicative of a power-law relationship. More detailed analysis is however needed before we can venture to use these results for extrapolation.

Interestingly, we find that a GBH based cut-off leads to a higher number of species than a height-based cut-off. As seen in Figure 3, the curve depicting the number of species as a function of the number of individuals obtained from a girth-based cut-off lies entirely above the one corresponding to a height based cut-off. This patterns too could only be meaningfully discussed when a comparison with other datasets is possible.

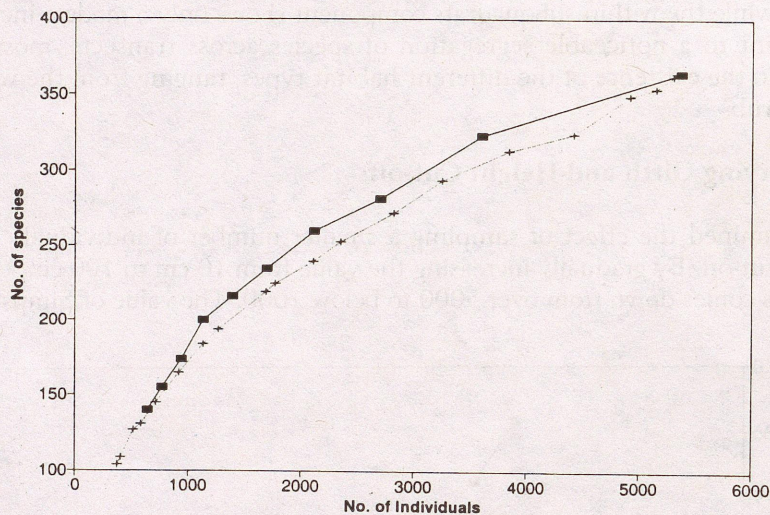


Figure 3. Number of species recorded in the samples as a function of the number of individuals in the sample. The upper curve (solid line, filled squares) corresponds to a girth-based selection of trees, while the lower curve (dotted line, + symbol) represents samples obtained from a height-based cut-off.

## DISCUSSION

There is some discrepancy between the formulation described by Lande (1996) and the traditional ANOVA computations. In particular, single classification ANOVA for unequal sample sizes involves computation of  $n_0$  (Sokal and Rohlf 1995) the 'effective' sample size, which is then used for estimating the between-groups variance. There is no analogous step in Lande's formulation. The between-transection component of variance computed using the ANOVA approach is found to be 9.87%, which is close to, but not identical to, the 10.63% obtained using Lande's approach. It can be easily seen that when the number of individuals and number of groups are large, the two methods would converge to the same value. In other circumstances, however, the differences between the estimates obtained by the two approaches could be substantial.

In fact, when the ANOVA approach was used to estimate the between-quadrat and within-quadrat variances components, the lack of concordance between the two methods was quite evident. The Pearson correlation between the values of the within-quadrats components obtained by the two approaches was 0.857. In fact, for nine out of the 60 transects, the assumption of added between-quadrats variance could not be sustained; the value of Mean Squares (MS) between-quadrats was actually smaller than that of MS within-quadrats. The mean value of the between-quadrats component of variance for the remaining 51 transects was 4.5%, about half of that obtained by Lande's approach. These differences suggest that a more careful scrutiny of the theoretical underpinnings of the two methods for deciding upon the suitability of one over the other may be worthwhile. As of now, we feel that Lande's approach based on Simpson's index of diversity may be adequate for a quantitative description of the partitioning of diversity.

One of the important findings of this study is the substantial difference between the between-transect variance of density (number of individuals per unit area) on one hand and of species diversity on the other; nearly 80% of the density variance is between-transects, in contrast to only 10% for species diversity. Also interesting is the fact that girths and heights of trees seem to follow the pattern of species diversity in this regard, and not so much as that of density. A more appropriate parameter than girth would be the basal area, and the between-transect component of basal area is found to be 9.7%, a value close to that obtained for species diversity. Whether these findings are widely applicable or not can only be judged by comparing them with those obtained from other datasets. Such studies are in progress.

The values of alpha- and beta-diversity as they are normally expressed are not in the same units; alpha diversity, for example, is often described as species richness, and beta diversity as the proportion of unshared species. As Lande (1996) has pointed out, the between-transect and within transect diversity would form better and more logical indices of alpha and beta diversity. We have examined the correlations between the values of beta diversity between pairs of transects as obtained using the above method, and those obtained using the percentage of unshared species (Jacard index, Ludwig and Reynolds 1988). The correlation was poor, suggesting that these two probe different aspects of turnover. When chord index (Ludwig and Reynolds 1988) was used as an index of beta diversity, its correlation with between-transect variance was 0.85. This is a high value no doubt, but still seems to leave some room for suggesting that the between-transects variance may still be probing a slightly different aspect of diversity. In particular, the Jacard index ignores the abundances of the species altogether, while the chord distance ignores the relative abundance of the two transects. A distance measure based on Simpson index thus seems to be more comprehensive, and may be more appropriate on this ground as well.

In summary, we have described the method of estimating the partitioning of species diversity into within-sample and between-sample components, using trees in the Nilgiri Biosphere Reserve as an example. For our data, we find the estimate of between-transect diversity to be quite robust against varying levels of sampling effort. Further investigation using other taxa such as birds and butterflies, using transects located across the entire Western Ghats, and using higher taxonomic categories such as genera and families, are in progress.

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