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[1].

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[2]. 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[3–5]. 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

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

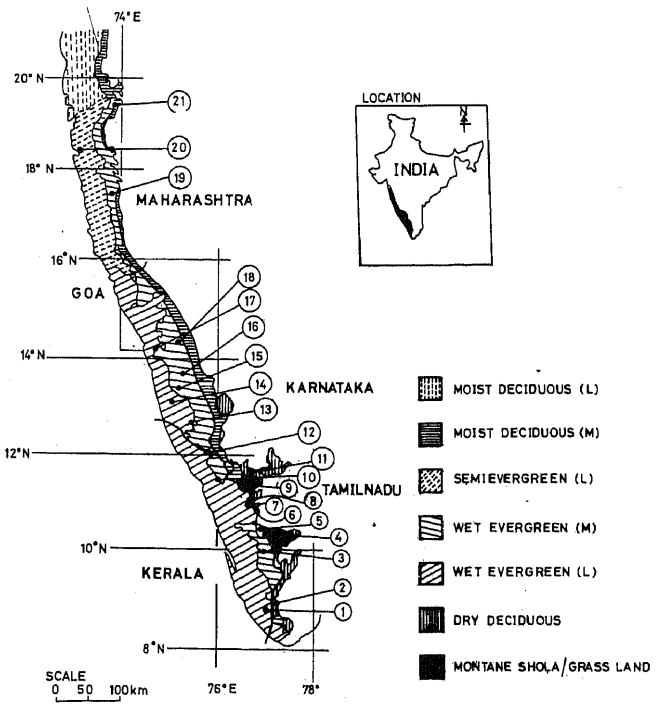

Figure 1. Sampling locations. Latitude, mean altitude, and mean rainfall in parentheses. 1, Bonakkad (8°38′, 300 m, 250 cm); 2, Cuttlam (9°, 1200 m, 150 cm); 3, Pooyamkutti (10°08′, 200 m, 300 cm); 4, Eravikulam (10°20′, 2100 m, 400 cm); 5, Topslip (10°26′, 800 m, 180 cm); 6, Walayar (10°50′, 100 m, 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).

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
Rarified 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[6]. A total of 508 species of birds were reported from south western India which include 144 species of water birds also[7]. 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[8–10] 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[11] 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).

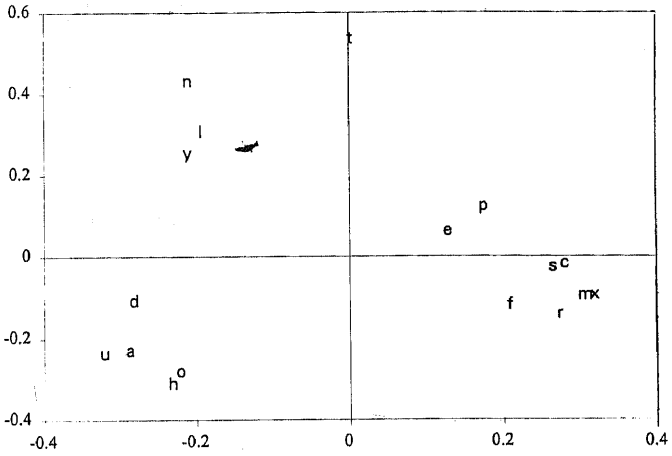

Figure 2. Two-dimensional representation of 13 transect level community attributes and 4 site attributes. u, Mean ubiquity; a, Median ubiquity; d, Standard deviation of ubiquity; h, Mean hospitality; o, Median hospitality; e, Evenness; p, Population of birds; f, Fisher's alpha; s, Species richness; c, 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.

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[12] 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 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-

curring 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

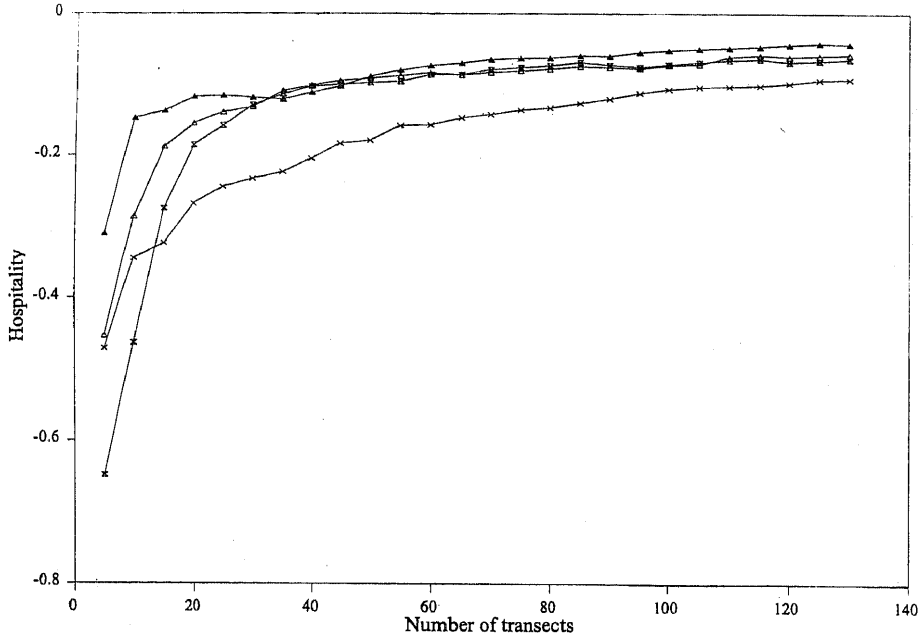

Figure 3. Hospitality as a function of number of total transects considered for four different transects selected at random.

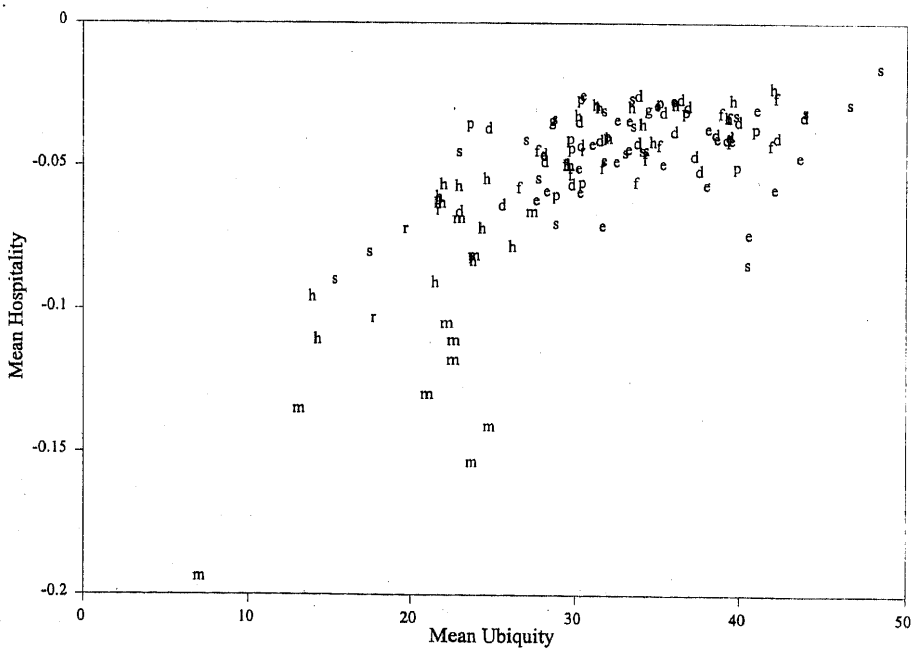

Figure 4. Mean hospitality as a function of mean ubiquity. Labels as in Table 1.

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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