Diversity of species assemblages of islands: Predictions and their test using tree species composition of shola fragments

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Based on all possible combinations of species that can theoretically exist on islands of different sizes, we estimated similarities among islands of equal size in their species compositions. We found that similarity coefficients among islands of equal sizes increases and the coefficients of variation for similarities decreases with increase in the size of islands. Accordingly, it can be predicted that the species compositions of small fragments shall be more diverse compared to large fragments. We tested this prediction using the tree species composition of the shola fragments at BR Hills, Western Ghats. Similarities among sholas were measured as coefficients of correlation between the frequencies of species in them and also as proportions of species shared among sholas. Small sholas were less similar and shared fewer species among themselves, compared to medium and large sholas. Also, small sholas showed higher coefficient of variation for the correlation coefficients and for proportion of species shared than medium or large sholas. In other words, species assemblage diversity among sholas was found to decrease with their size and large islands appeared to converge towards a common assemblage of species. Based on our results, we argue that small fragments add structural and functional heterogeneity to the ecosystem and hence are as important as are the large fragments in conserving biodiversity.

THE island Biogeography (IBG) theory proposes that the number of species on an island increases with the size of the island[1]. The argument is based on the assumption that the rate of immigration of species decreases and that of local extinction increases with increase in the number of species in the island (Figure 1). Consequently, the theory predicts, islands attain equilibrium with respect to the number of species they can harbour and this number is found to increase nonlinearly with the size of the islands[2–7] (Figure 1). Such nonlinear relations between the number of species and the size of the islands, otherwise known as the 'species area curves', have been repeatedly demonstrated in several situa-

tions[2–10]. Though the IBG theory has strong predictive power for the number of species on an island, it states nothing about the composition of the species in the islands.

The process of development of islands suggests an entirely different state of equilibrium with respect to the composition of the species[4,11]. Three distinct stages are recognized during the development of an island. During the initial non-interactive stage (stage 1), the island is invaded by a greater number of species than can eventually be sustained on the island. These species exist as long as their populations are small and hence do not interact among themselves. Once the populations build up, the species begin to interact, resulting in the competitive exclusion of some and dominance of others.
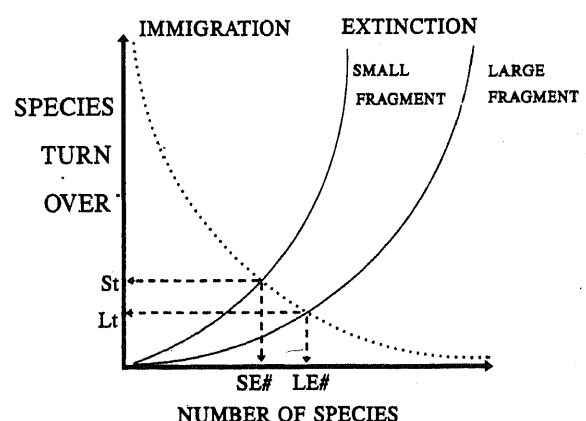

Figure 1. Interaction between the immigration and extinction resulting in an equilibrium number of species in an island. As argued by McArthur and Wilson[1], the rate of immigration decreases and that of extinction increases with the number of species in an island. But the extinction rates are additionally influenced by the size of the island; the smaller islands experience a higher rate of extinction and turnover (St) than the larger islands (Lt) and hence harbour lesser number of species at equilibrium (SE# compared to LE# in large islands). This results in the familiar species area curves.
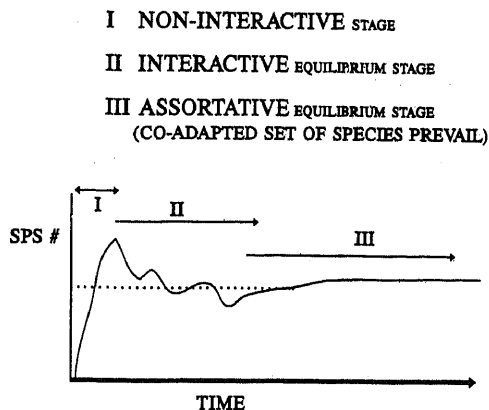
I **NON-INTERACTIVE** STAGE

II **INTERACTIVE** EQUILIBRIUM STAGE

III **ASSORTATIVE** EQUILIBRIUM STAGE
(CO-ADAPTED SET OF SPECIES PREVAIL)

Figure 2. Three distinct stages of the process of development of an island (developed based on the details given by Dickerson and Robinson[4]).

This process generally leads to a decrease in the number of species (Figure 2). The local extinction and immigration occurring during this interactive phase (stage 2), begin to stabilize the species numbers at a level that can be sustained on the island. During the process, however, owing to the repeated immigrations and extinctions, a set of species become co-adapted and get established on the island. Such an island becomes relatively immune to subsequent immigrations. This state called as the 'assortative equilibrium stage' is relatively stable over long periods of time (stage 3). The species on the island are further subjected to the process of natural selection.

Thus while the IBG theory predicts that islands of a given size harbour similar numbers of species, the process of development of islands suggests that they might exist in several states of assortative equilibria. The diversity of these states is an important component of the ecosystem biodiversity because beside adding to the heterogeneity, each of these states could have distinct functional properties[12]. For instance, two similar sized islands each with three but different species of plants (e.g. ABC and BCD) could harbour entirely different kinds of insects; in fact both islands together might harbour a set of arthropods different from that of another relatively larger island with all the four species (ABCD) in it. Thus in the context of conserving biodiversity, species composition of islands and their heterogeneity could be as important as the numbers in these islands.

Although the islands are suggested to exist in diverse states of assortative equilibrium, as of yet, there are no predictions on how diverse these states would be among a set of similar sized islands. In this paper we derive the relation between the diversity of such assortative equi-

librium states (AES) and the island sizes. Based on the possible combinations of species an island can theoretically harbour, we show that the diversity of species compositions decreases with increase in island size and hence argue that small fragments are as much worth conserving as are the large fragments. We also test these relations derived using the data on the tree species compositions of the sholas, the high montane natural forest fragments occurring along the Western Ghats, South India.

Types of AES and the island size

Let us assume an area with a number of interacting islands of different sizes which together contain a global set of N species. The IBG theory suggests that the number of species increases with the size of the island. Accordingly, islands exist with different numbers of species ranging from one per island (the smallest) to N per island (the biggest island) and all islands of similar size harbour comparably equal number of species, but may contain different combinations of species. For instance, the smallest islands with only one species in each of them can occur in N different types while the largest islands shall have all the N species in them and hence would be of only one type. For other islands containing > 1 and $< N$ species, the number of different combinations of species that the islands could contain can be computed as

$$N_{(n)} = N_{c_n},$$

where $N_{(n)}$ is the number of different combinations of species possible for islands containing n species in them. Accordingly for a given global set of N species, the number of possible combinations of species increases up to a certain size of the island and then decreases. To be precise, the number of the species combinations increases up to island size that contain $n = N/2$ if N is even and $n = ((N \pm 1)/2)$ if N is an odd number and then decreases. For instance, for $N = 10$, the number of such combinations increases to 252 when $n = 5$ and then decreases (Figure 3).

Thus the possible combinations of the species (the frequencies) initially increase and then decrease with the size of the island. These combinations computed here are exhaustive and inclusive of, but do not represent the eventual AES. Nevertheless since the AES are likely to be a (probably random) sub set of these combinations, their relative frequencies can be reflected by these exhaustive combinations. In other words, the relation between the frequencies of different AES and the island sizes could also be expected to be similarly non-linear.
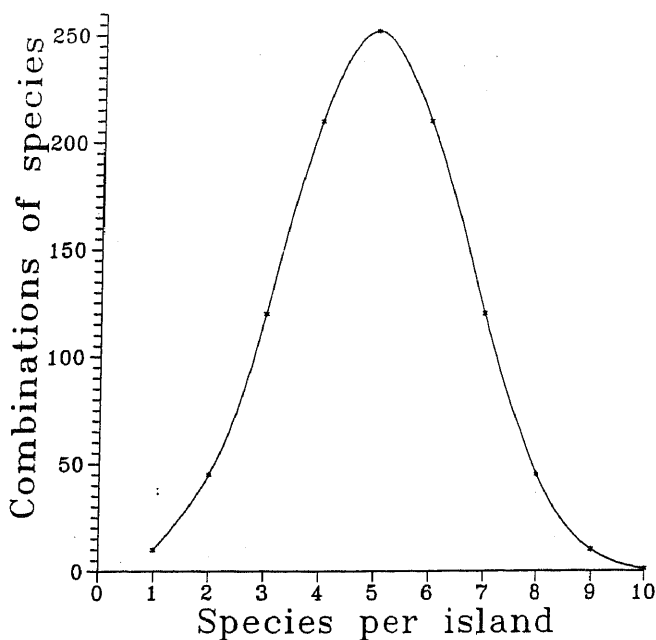
Figure 3. The frequency distribution of the number of combinations of species possible in islands containing varying number of species in them. Though the distribution shown here refers to the combinations possible from a global set of 10 species, the pattern remains the same for other values of global set.
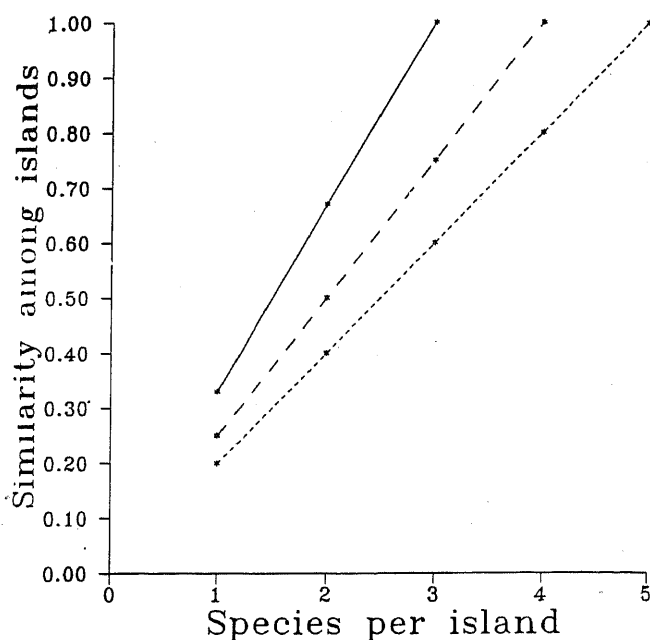

Figure 4. Similarity among islands of the same size containing combinations of species from the global set of 3 (solid line), 4 (dashed line) and 5 (dotted line) species.

Diversity of AES and island sizes

Similarity among islands

The foregoing suggests the possible relation between the numbers of equilibrium states and the island sizes. From this we derive the relation between similarity among the equilibrium states and the size of the islands. We computed the average similarity between any two randomly selected islands of a given size as the proportion of the species shared between them. Such similarity reflects the extent of diversity among the AES; lesser the similarity, the more diverse they are. We have computed these similarities for all combinations of species (n; sizes of islands) possible for each of a range of N values. It turns out that the similarities thus computed among the islands of similar sizes increase linearly with the size of the island at the rate of $1/N$ (Figure 4) as shown below.

Consider two islands containing $n1$ and $n2$ species. The probability that a given species is found in both islands is ($n1 n2/N^2$) and hence the number of species common between them would be ($n1 n2/N$). Let us define the similarity as the ratio of species found common between them to that of the average of the species in them. This similarity is given by

$$\text{Sim} = 2n1n2/N(n1 + n2). \tag{1}$$

If the islands are of similar size with $n1 = n2$, then

$$\text{Sim} = n1/N. \tag{2}$$

In other words for a given global set of N species the similarity among sholas increases with the size of the shola ($n1$) at the rate of $1/N$.

Thus the smallest islands are least similar (and hence more diverse) among themselves compared to large islands; the largest islands shall always be similar among themselves as they contain the complete set of N species in them. Again this relation could persist for assortative equilibrium states as they constitute a (probably random) subset of these combinations. Accordingly we derive the following prediction:

Prediction 1. The similarity among the AES of a given size increases with the size of the islands; or the diversity among similar sized islands decreases with the island size.

Variance for similarities among islands

As the size of the island increases, the proportion of the global set of species occurring in them also increases. Consequently, large islands not only shall be similar among themselves, but the variance for their similarity shall be less. On the other hand among smaller islands, there could be some that are highly similar and others that share no species at all among them. This results in a high variance for the similarities among small compared to large sholas. Such increased variance of small islands

also reflects the high diversity among their AES. Thus while the similarity among islands increases, the variance for similarity values decreases with the size of islands. Therefore we derive the following second prediction:

Prediction 2. The coefficient of variation of the similarities among sholas of similar sizes decreases with the size of the islands.

Test of the predictions

Testing these predictions has two different problems: a) It is difficult to estimate the complete set of species occurring in an area and hence also to estimate the combinations of species expected in different fragments; b) The maximum number of combinations of species possible ($N(n)$ max) increases exponentially with N, the total species in an area. For instance, for values of N as low as 10, there are 252 combinations possible for fragments containing 5 species each. Thus for an area having several tens of species (which is very common with most taxa in most tropical forest ecosystems), the $N(n)$ max combinations are extraordinarily high. Thus even if the assortative equilibrium states constitute a small proportion of these combinations, the sample sizes required to capture all of them will be enormously high and might be a difficult proposition. Therefore we attempted for a qualitative test of the predictions though for prediction 1, we also attempted a quantitative test based on equation (1) above.

Methodology

We tested these predictions by studying the tree vegetation composition of sholas, the high montane natural fragments occurring along the Western Ghats. The sholas are apparently one of the appropriate systems because they occur in varied sizes and shapes with varying degrees of isolation and are existing for at least a few centuries in relatively undisturbed states at higher altitudes. Consequently they have had enough time and opportunities to develop into assortative states. The study was conducted in the Biligiri Rangan Swamy Temple (BRT) wildlife sanctuary (77°00'E 11°45'N to 77°15'E 12°10'N) along the eastern edge of Western Ghats, where sholas occur at an altitude of 1400 to 1600 m. Two areas of 5 × 5 km each were marked off at the southern and northern part of BR Hills wildlife sanctuary and 28 and 17 sholas occurring in these areas respectively were identified for the study. The two study areas, hereafter called Jodugere and Gummane Sholas were separated by about 25 km. The data from the two areas were not pooled so as to avoid the possible con-

founding of the geographical differences; indeed the sholas differed in their species compositions. In both the areas, sholas were classified into three size categories, viz. small, medium and large (Table 1). Varying number of grids of 10 × 10 m were laid randomly within each shola and the trees (> 1 cm DBH) were enumerated. From this data, the relative frequencies of the trees and species composition of the sholas were determined. Two parameters were computed to represent the similarity among sholas of a size class: a) the proportion of the species shared between any two sholas was computed as a ratio of the number of common species to that of the maximum number of species in either of the two sholas; b) the correlation coefficients of the frequencies of species between any two sholas of a given size category.

Results

As expected, the number of species increased with the size of the sholas at both study areas (Table 2); the large sholas had over twice the number of species in the small sholas. The species area relation also showed the expected nonlinear increase in the number of species with the size of the island (Figure 5 for Jodugere sholas; data not shown for Gummane sholas). Nevertheless the two

Table 1. Numbers and area of the sholas sampled and the grids laid in them at Gummane and Jodugere areas. Values in parentheses are ranges

Shola size	Area (ha)	Jodugere		Gummane	
		Number of sholas (n)	Grids/ shola	Number of sholas (n)	Grids/ shola
Small	<1	17	5.17 (4–9)	5	6 (4–12)
Medium	3–5	8	18.4 (16–23)	7	7 (5–12)
Large	>10	4	30.5 (16–23)	6	14.8 (11–23)

Table 2. Number of species per shola and the total species recovered in sholas of different size classes at Gummane and Jodugere areas. Values in parentheses are ranges

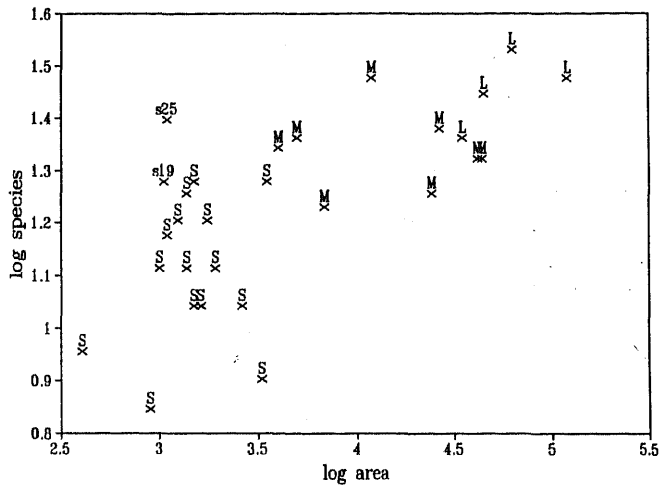| Size class	Jodugere		Gummane	
	Species/ shola	Total species	Species/ shola	Total species
Small	13.65 (7–19)	43	16 (15–17)	39
Medium	21.87 (17–30)	47	23.85 (21–27)	48
Large	28.75 (23–34)	45	35.5 (31–40)	53

Figure 5. Relation between the log number of species and the log area of the sholas at the Jodugere area. ($Y = 0.595 * Å.174$). S, Small sholas; M, Medium sholas and L, Large sholas.
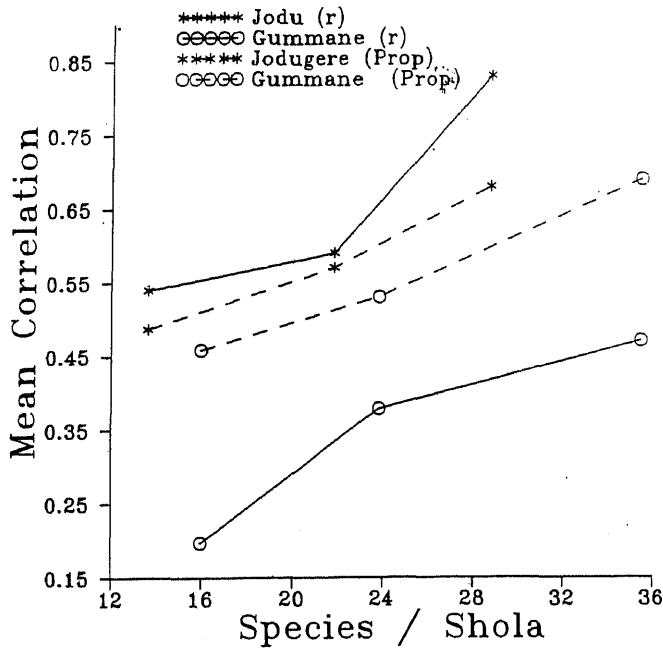

Figure 6. Relation between the similarity parameters and the size (average number of species per shola) class of the sholas for Jodugere (asterisk) and Gummane (open circle) areas. Similarity parameters are the proportion of the species shared (dashed line) and correlation coefficient (solid line) among sholas of a given size category.

a

b

Figure 7. Relation between the expected and observed similarities among all possible combinations of sholas of a, Gummane and b, Jodugere areas. The lower solid lines in both the figures represent the predicted relation between the expected and observed values (regression coefficient = 1). The line amidst the points refer to the best fit line with $Y = 018 + 0.90*X$; $r = 0.684$; $df = 151$; $P < 0.001$ for Gummane area. $Y = 0.43 + 0.43 *X$; $r = 0.37$; $df = 404$; $p < 0.001$ for Jodugere area.

cantly. Therefore further comparisons among the shola size classes are made separately for the two areas.

Prediction 1

The proportion of species shared among the sholas of a given size category increased with the size in both Gummane and Jodugere areas (Figure 6). Similarly the correlation coefficients among sholas of a size category also increased with their size (Figure 6). Thus it appears that small sholas are more diverse among themselves than are the large sholas. In other words, as predicted, the similarity among the islands increases with their sizes.

study areas differed for total number of species recovered in them (Table 2). The study areas are separated by a distance of about 25 km and have different kinds of forests flanking them. Sholas at the Gummane area are surrounded by the moist deciduous forests while those at Jodugere by the evergreen forests; also, probably for this reason, their species compositions differed signifi-
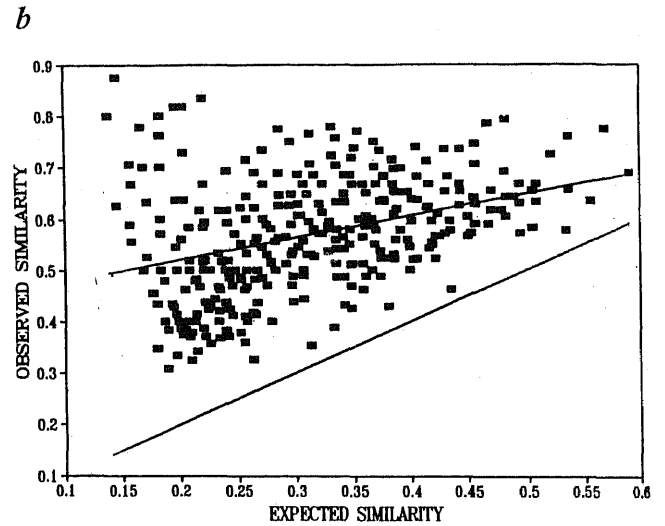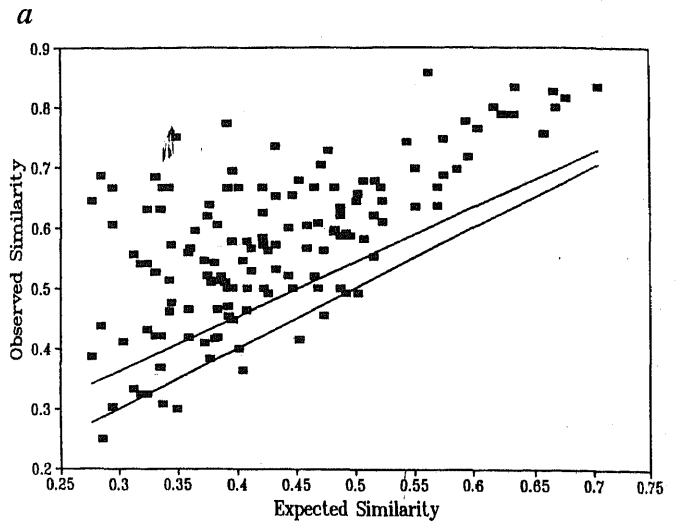
Table 3. Correlation coefficients and proportion of species shared among the sholas of the three size class

Size class	n*	Gummane Correlation Mean	Correlation CV	Proportion sps shared[@] Mean	CV	n*	Jodugere Correlation Mean	Correlation CV	Proportion sps shared[@] Mean	CV
Small	10	0.19	129.25	0.45	34.14	136	0.54	43.43	0.48	29.05
Medium	21	0.37	62.56	0.53	15.96	28	0.59	30.18	0.58	13.60
Large	15	0.52	55.13	0.69	19.62	6	0.83	7.33	0.68	9.20

*n refers to the number of pairs of sholas used for computing the parameters.
[@]Proportion species shared is computed as the ratio of number of species shared between the sholas to that of the maximum number of species found in either of the sholas.
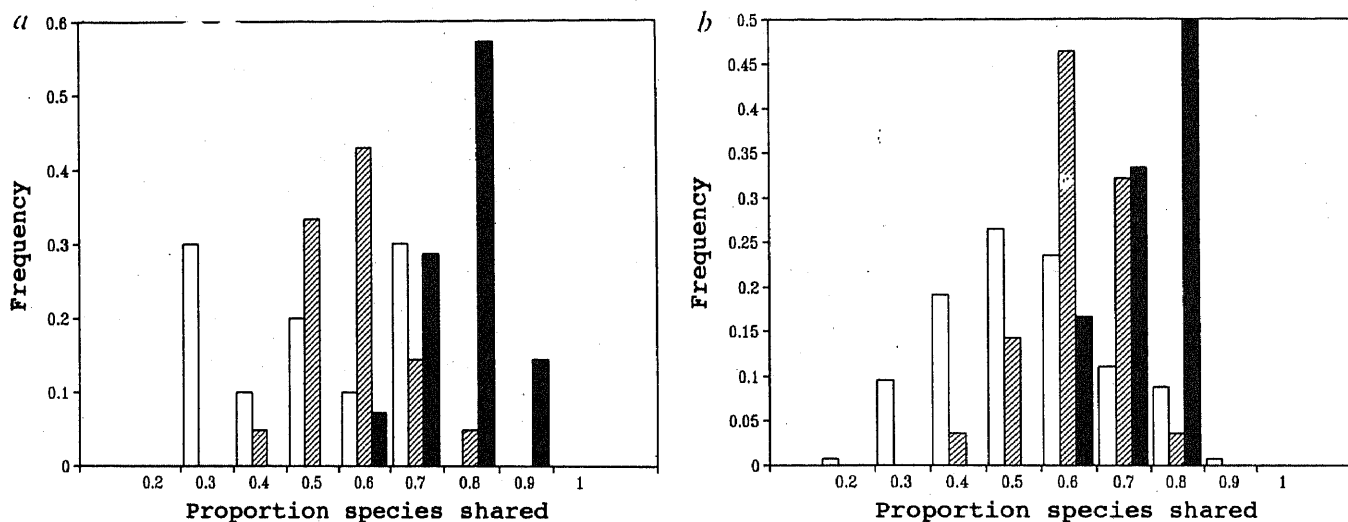
Figure 8. Frequency distribution of proportions of species shared among sholas of large (shaded histogram), medium (hatched histogram) and small (open histogram) at a, Gummane and b, Jodugere areas.

The proportions of species shared between pairs of sholas were plotted against those expected based on equation (1) above. At both Gummane and Jodugere areas, similarities among sholas increased with the size of the sholas (Figure 7 a, b) though the observed similarities were more than expected, suggesting that certain species tend to co-exist and do not assort randomly – a probable evidence of assortative equilibrium states.

Prediction 2

Coefficients of variation (CV) for both correlation coefficients and for the proportions of species shared were higher for small than large sholas (Table 3) in both study areas. The CV for these similarity parameters for medium sholas was in general between the other two size categories. The decrease in the variance for the similarities with the size of the sholas is also evident from the frequency distribution of the proportions of the

species shared (Figure 8 a and b). The small sholas differ widely for the proportions of species shared among themselves compared to medium and large sholas. At Jodugere for instance, the proportions of species shared among large sholas were highly negatively skewed and ranged from 0.60 to 1.00, while those among small sholas were normally distributed and ranged from 0.2 to 1.0; the similarity values among medium size sholas were in between. Thus the data supports the second prediction that CV for similarity values decreases with the size of the islands.

Discussion

Our results suggest that the diversity of species assemblages of sholas decreases with size of the sholas, supporting our predictions. It should be noted that these predictions are applicable even if the islands have not attained assortative equilibrium states because they are

derived based on the exhaustive combinations of species assemblages. In other words, the relation suggested by the predictions is true even during the initial dynamic period of island developments.

In another study we (Ganeshaiah et al., communicated) have shown that the observed differences between the small and large sholas are not because of the stochastic consequences associated with the fewer grids sampled from small sholas. In fact sampling equally fewer grids from large sholas did not reduce the similarities among them to that observed among small sholas. Thus the observed patterns do not seem a consequence of the sampling regimes but due to the development of diverse equilibrium states among the small compared to large sholas. Large sholas seem to converge towards a common equilibrium state. The results suggest that small fragments though individually may not be species-rich compared to large fragments, together they add substantially to the spatial and structural heterogeneity of the ecosystem that might be important for its functional diversity[12]. These patterns, however, may not be true for all the organisms. Large vertebrates with a very wide home range, for instance, cannot be expected to show such relations. On the other hand these relations might not be uncommon for a number of lower organisms such as bacteria, fungi, and lower vertebrates and invertebrates, that require small areas for their survival.

As argued earlier, if the specific combinations of host plants are important in harbouring specific arthropods, or invertebrates or fungi or bacteria, then the heterogeneity observed among small sholas is as much important as increasing the species richness of the ecosystem in conserving biodiversity. In other words, we suggest that the structural heterogeneity added by small islands is a different but a very important component to be considered while formulating the biodiversity conservation strategies. In this sense small islands or fragments are as important as the large fragments and are hence worth conserving.

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