

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.

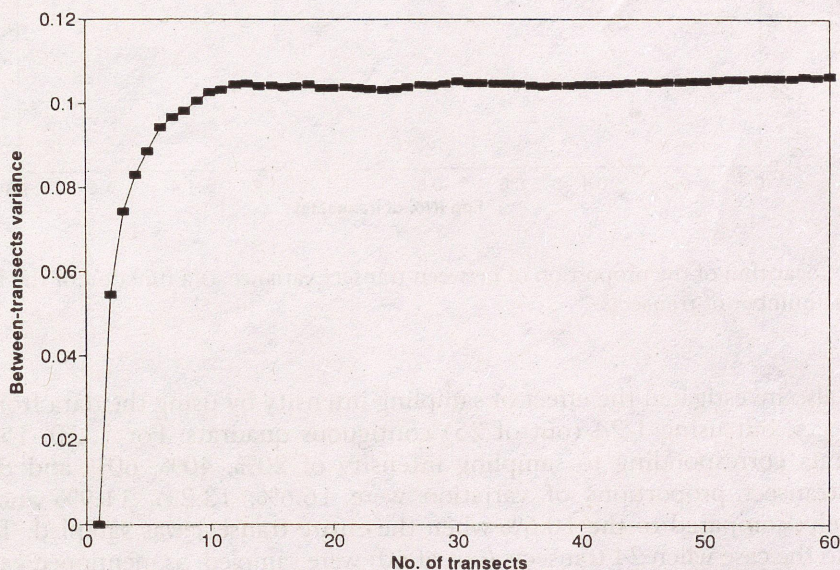


Figure 1a. The proportion of between-transect variance as a function of the number of transects.

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 sampled by the three approaches.

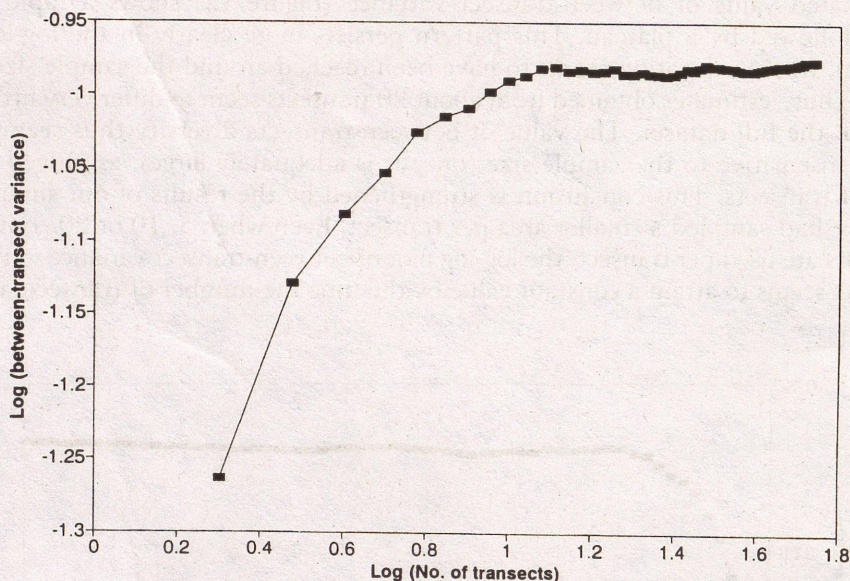


Figure 1b. Logarithm of the proportion of between-transect variance as a function of the logarithm of the number of transects.

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,

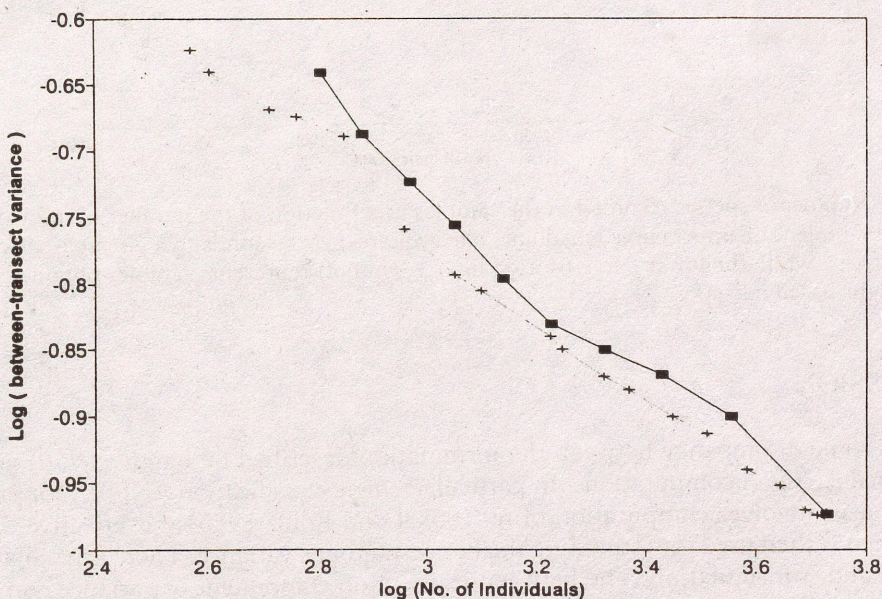


Figure 2. Logarithm of the proportion of between-transect variance as a function of the logarithm of the number of individuals sampled. The upper curve (solid line, filled squares) corresponds to a girth-based selection of trees, while the lower curve (dotted line, + symbol) represents samples obtained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

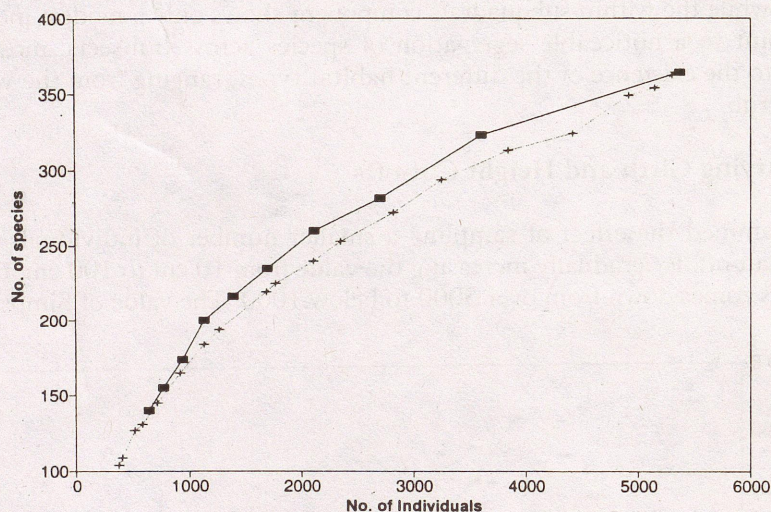


Figure 3. Number of species recorded in the samples as a function of the number of individuals in the sample. The upper curve (solid line, filled squares) corresponds to a girth-based selection of trees, while the lower curve (dotted line, + symbol) represents samples obtained from a height-based cut-off.

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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