Avalanche index: A new measure of biodiversity based on biological heterogeneity of the communities

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A variety of indices are available to quantify the diversity of biological communities. All these indices assume that biological diversity can be satisfactorily described by two major components viz., the number of species and their relative abundances. These indices treat all species as equivalent and ignore taxonomic, morphological, or any such biological differences among species of a community. However, two biological communities with similar number and frequencies of species could differ, for instance, with respect to the taxonomic diversity of the constituent species. A common opinion among ecologists has been that any measure of biodiversity should incorporate biological differences among species or the heterogeneity of the community as an important component. In this paper we propose a new measure of diversity, the 'Avalanche index', which in addition to species numbers and frequencies, also uses the biological and ecological differences among species comprising a community. The index attempts to integrate, over all possible species combinations, the biological differences among species in proportion to their frequencies in the community. We use this index to measure the biodiversity of a set of samples of dung beetles and discuss its merits and problems compared to other indices that are being widely used.

MEASURING biodiversity of a habitat or community has been one of the central issues of ecology and conservation biology both because of its academic necessity and because of its utility in devising conservation strategies. Nevertheless, measuring biodiversity has not been easy and has remained a challenging task even after 15 years of the first use of the term[1]. Though one of the simple methods suggested is to count the number of species in the habitat or community[2], such an approach turns out to be too simplistic as it does not account for the extent of representation of each of these species in the community. For this reason, a wide variety of indices have been developed to describe diversity mainly based on the number, and frequencies, of the species; these indices differ only with respect to the weightages given to the second of these components while combining them into a single value[3].

The most popular and widely used measures are Shannon's, Simpson's, and Fisher's alpha-log series[3]. There is, however, a great deal of disagreement over their efficiency in reflecting the biological diversity[3]. One of the major problems is, they all assume that 'all species at a site, within and across systematic groups contribute equally to its biodiversity'[1].

In other words, the existing indices ignore biological, ecological and functional differences among species. Consider two communities both with equal number (and similar frequencies) of species but one of them has all the species belonging to the same genus while the other has its species from different genera or families or orders. The latter community would be biologically more diverse because such taxonomic diversity among species would be associated with their morphological diversity or character diversity[4], and diversity in their ecological roles. Such diversity in taxonomic, morphological and any biological features of the species of the community needs to be reflected in any measure of biological diversity. Unfortunately, existing indices do not incorporate these components of diversity[1,5]; in fact it has been suggested that 'a new calculus of biodiversity' needs to be developed[5].

In this paper, we propose a new index for measuring biological diversity that can incorporate as many details of biological differences among the species of a community as possible. The proposed index is constructed so as to reflect taxonomic, ecological, functional or any such biological differences among species of a community in addition to the species richness and their relative abundances. As a case study, we use this index for a data set on dung beetles and evaluate its merits with those of a few other indices being widely used.

The Index

The proposed index, 'Avalanche Index'[6], is based on the notion widely agreed upon that a community with certain number of species differing highly on taxonomic, morphological and any such features is more diverse than another community with same number and frequency but with more similar species[1,2,5]. Hence the index was constructed such that interspecific differences within a community form an important component of the diversity. At the same time the proposed index also retains the features of the existing measures of diversity. Thus it has two components, viz. i) the distances among species of the community based on their taxonomic, morphometric and any such traits and ii) relative abundances of the species. Using these, the index arrives at a measure of biodiversity by integrating the product of the frequencies and the corresponding interspecific distances over all possible species combinations. Thus the Avalanche index (AI) is given by

$$\mathrm{AI}=\sum_{i=1}^{n}\sum_{j=1}^{n}(P_i d_{ij} P_j), \tag{1}$$

where P_i and P_j are frequencies of ith and jth species and,

$$d_{ij}=\left(\sum_{k=1}^{c}(X_{ik}-X_{jk})^2\right)^{1/2}. \tag{2}$$

X_{ik} and X_{jk} are the values of the ith and jth species for kth character and c is the number of traits on which information is available. Note that, as constructed, the AI essentially reflects the average distance between any two randomly chosen individuals of the community. The distance component d_{ij} increases with c and hence it might be appropriate to use an average estimate of d_{ij} such that AI values across studies could be compared. However, for the present study we have retained d_{ij} as such.

Table 1. Correlation of Avalanche index with other indices of diversity computed for dung beetles collected from 12 samples of cattle dung around Bangalore. The values below the diagonal are the correlation coefficients

	S	H'	$1/D$	α	AI	$\mathrm{AI_t}$	$\mathrm{AI_m}$	$\mathrm{AI_f}$
S		**	*	**	**	*	**	**
H'	0.72		**	**	**	**	**	**
$1/D$	0.51	0.90		*	**	**	**	**
α	0.98	0.78	0.62		**	*	**	**
AI	0.80	0.96	0.86	0.85		**	**	**
$\mathrm{AI_t}$	0.56	0.97	0.92	0.64	0.92		**	**
$\mathrm{AI_m}$	0.80	0.95	0.84	0.86	0.99	0.89		**
$\mathrm{AI_f}$	0.77	0.94	0.83	0.80	0.95	0.90	0.92	

*$P < 0.05$; **$P < 0.001$.

S, Species richness; H', Shannon index; 1/D, Simpson index; α, Fisher's alpha-log series; AI, Avalanche index considering taxonomic, morphological and functional traits together; $\mathrm{AI_t}$, Avalanche index computed considering only taxonomic differences; $\mathrm{AI_m}$, Avalanche index computed considering only morphological differences; $\mathrm{AI_f}$, Avalanche index computed considering only functional differences.

A case study

We attempted to evaluate the AI with others by comparing diversity of dung beetles in 12 samples of cow dung collected from rural areas between 19 October and 9 March 1997. Only those pats aged 3–4 days were collected from fallow lands, around irrigation channels and other agricultural areas where cattle grazed regularly. The number of dung pats in each sample, species of dung beetles and their abundances are presented in Appendix 1. Using this data, four diversity indices, viz. Shannon's, Simpson's, alpha-log series and Avalanche Index were computed for all the samples.

Computation of AI

The crucial step in computing AI is estimating the distances among species. In the present study with dung beetles, we used taxonomic, morphological and functional traits to measure the distances between any given pair of species in a sample (Appendix 2). Taxonomic distance (X_{ik}–X_{jk}) was considered one if the i and j taxonomic units being compared differed at species, two if they differed at genus and three if they differed at family level. Quantitative morphometric traits were measured on at least five specimens and averaged (Appendix 2). These measurements were converted to z-scores for use in the calculation of the distance. Other qualitative traits were directly used (see Appendix 2). The traits termed 'functional' were chosen so as to indicate the way the beetles use and colonize the dung – their resource. These traits were also scored on a qualitative scale. The distances between each pair of species were computed using equation (2) and the Avalanche index using equation (1).

Results and discussion

AI was strongly correlated with other indices and so were other indices among themselves (Table 1). Such an association of the AI with other indices is expected because it retains their basic feature by incorporating the frequencies of species in it. In fact as long as the comparisons are made only at the species level (d_{ij} = 1, that is, if individuals differ at species level only) then the values of AI will be exactly similar to those of Simpson's index. The values of AI deviate only when the differences are considered above the species level or when other traits are also considered.

The Avalanche index differs from others in that probably for the first time it incorporates information on the interspecific distances and hence the biological

Table 2. Diversity indices of the 12 samples of cattle dung pats

		Samples												
		1	2	3	4	5	6	7	8	9	10	11	12	Total
Species richness	(S)	13	12	6	10	8	7	5	5	5	3	4	6	16
Total abundance	(N)	199	187	131	94	146	150	119	264	178	135	59	92	1754
Shannon index	(H')	0.669	0.660	0.470	0.764	0.645	0.207	0.258	0.383	0.114	0.139	0.502	0.582	0.706
Simpson index	($1/D$)	2.621	2.726	2.130	4.920	3.646	1.230	1.371	1.866	1.108	1.179	2.898	3.146	3.183
Log series	(α)	3.115	2.857	1.299	2.832	1.823	1.523	1.056	0.874	0.957	0.543	0.972	1.437	2.430
Avalanche index	(AI)	3.52	4.45	2.45	4.47	3.63	0.58	1.03	1.32	0.32	0.39	2.10	2.43	3.068
Taxonomic	(AI_t)	0.81	0.88	0.70	1.07	1.00	0.22	0.34	0.55	0.12	0.16	0.87	0.85	0.905
Morphological	(AI_m)	2.86	3.82	2.18	3.81	2.71	0.43	0.71	1.05	0.23	0.31	1.62	1.80	2.375
Functional	(AI_f)	1.73	1.92	0.74	1.70	2.09	0.28	0.62	0.58	0.17	0.17	0.95	1.33	1.505

Table 3. Mean, SD and coefficient of variations of different indices compared

Diversity index	Mean	SD	CV
H'	0.446	0.225	50.57
$1/D$	2.403	1.160	48.27
α	1.607	0.869	54.09
AI	2.223	1.528	68.74

heterogeneity within each community. This is clear from samples 1 and 2 which have comparable Shannon indices (0.67 and 0.66; Table 2) but differ with respect to AI (3.52 and 4.45; Table 2). This difference, we argue, arises from the ability of the AI to capture the inherent biological, morphological and functional heterogeneity among the species of the two samples. For instance, sample 2 has a relatively high frequency of *Onitis philemon* (0.149 compared to 0.05 in sample 1) which is taxonomically and morphologically different from others in the sample (see Table 4). Consequently its AI is relatively high compared to that of sample 1 (Table 2). This is also evident from the AI computed based purely on taxonomic, morphological or functional distances. In other words, AI also brings out the diversity contributed by the biological differences (distances) among the species in the community.

Further, AI also appears to have a better discriminatory ability among the samples. The coefficient of variation of the 12 samples was 69% for AI compared to 54% for Fisher's alpha-log series and 48% for Simpson's (Table 3). This means, AI helps in discriminating the communities more efficiently than other indices. Since this discrimination is a function of intra-community heterogeneity among species, it also helps in evaluating the biodiversity value of the communities. The discriminatory ability of the index is also evident by comparing the samples 10 and 11. The Shannon's and Simpson's indices of sample 11 were 3.6 and 2.5 times that of sample 10 while its AI is 5.4 times higher.

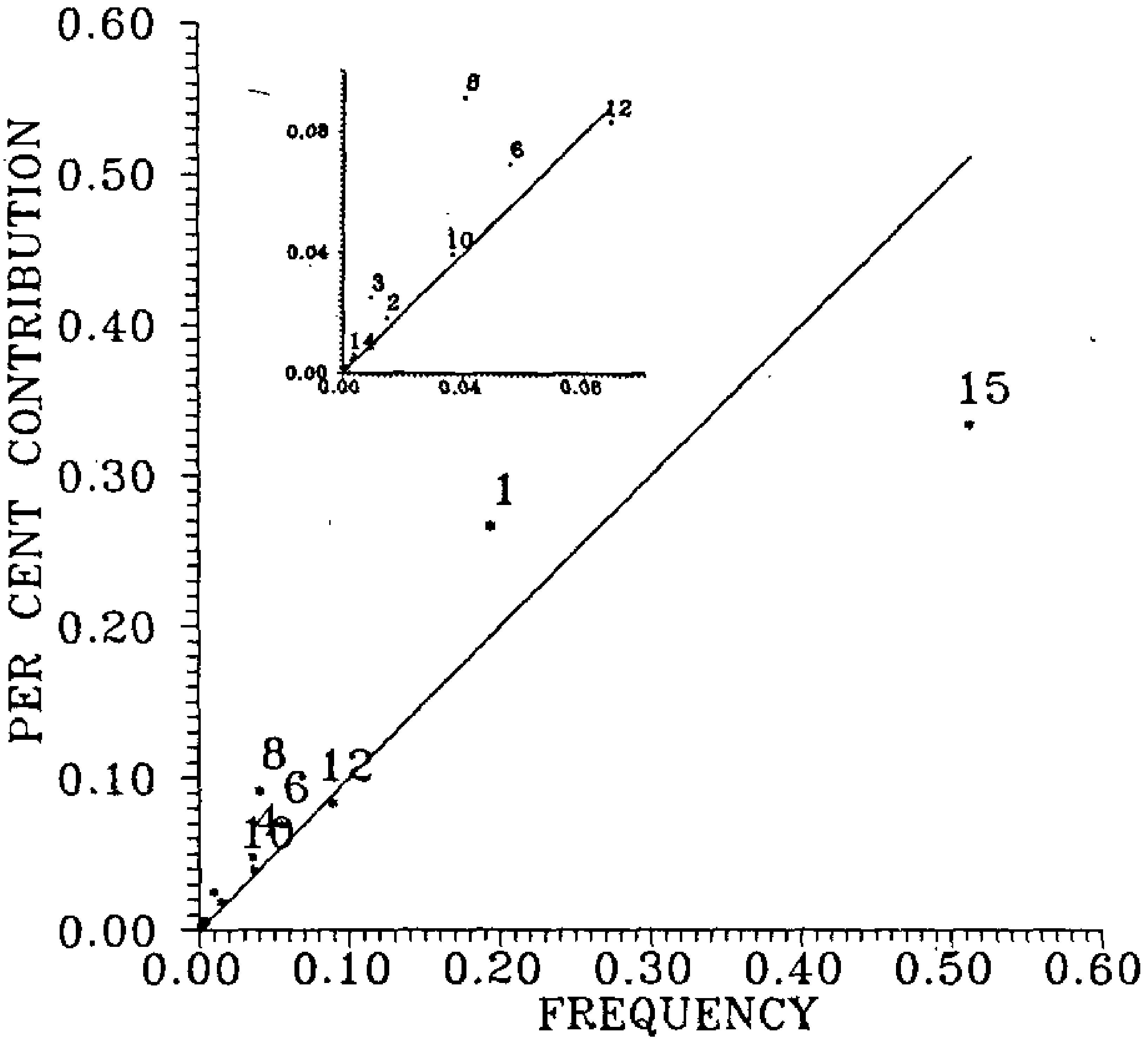

Figure 1. Relation between frequencies and relative contributions to Avalanche index of the 16 species. The numbers refer to the species in Appendix I. The lower end of the graph is scaled up in the inset for clarity. The solid line from the origin indicates the expected contribution of those species whose distance to others is unity.

Similarly, sample 5 is about 3 times that of sample 6 on Shannon's and Simpson's indices while it is about 6.3 times higher on AI. However there are also situations where the differences between samples are narrowed down on AI compared to other indices (samples 2 and 4). This would happen when the intra-community heterogeneity among the species is relatively higher for the sample whose Shannon's and Simpson's indices are low. Sample 2 is less even than the sample 4 and hence its Shannon index is lower (0.67) compared to sample 4 (0.76). Nevertheless the heterogeneity of species within sample 2 is higher which enhances its AI (see Appendix 1). In other words, the narrowing of the differences

Table 4. Matrix of distances between species of dung beetles

Species	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Mean
1	3.07	11.23	4.03	7.59	6.27	5.9	9.85	6.98	5.82	8.21	4.77	6.28	6.33	4.78	5.38	6.43
2	–	10.18	2.74	6.63	5.03	4.38	8.89	5.92	4.42	7.09	3.89	4.41	4.59	3.75	3.75	5.25
3		–	9.59	5.88	6.94	8.93	3.82	5.37	6.62	4.45	7.43	7.02	7.74	8.24	8.29	7.45
4			–	5.72	4.42	3.95	8.64	5.7	4.64	6.59	4.21	4.43	3.8	3.97	3.62	5.07
5				–	4.46	5.61	5.65	3.53	4.37	3.69	4.79	4.51	3.88	5.09	5.24	5.11
6					–	2.61	5.93	4.1	3.21	4.55	3.23	2.94	3.5	3.26	3.63	4.27
7						–	7.87	5.35	4.15	6.19	4.02	3.41	3.43	3.32	3.8	4.86
8							–	4.9	5.16	4.24	5.99	5.71	7.19	6.82	7.11	6.52
9								–	2.97	2.44	3.33	3.53	4.1	3.97	4.76	4.46
10									–	4	1.92	1.88	3.75	2.59	3.44	3.93
11										–	4.38	4.15	4.95	5.19	5.36	5.03
12											–	2.69	4.13	2.23	3.53	4.04
13												–	3.16	2.81	3.01	4.00
14													–	3.67	3.39	4.51
15														–	3.38	4.21
16															–	4.55

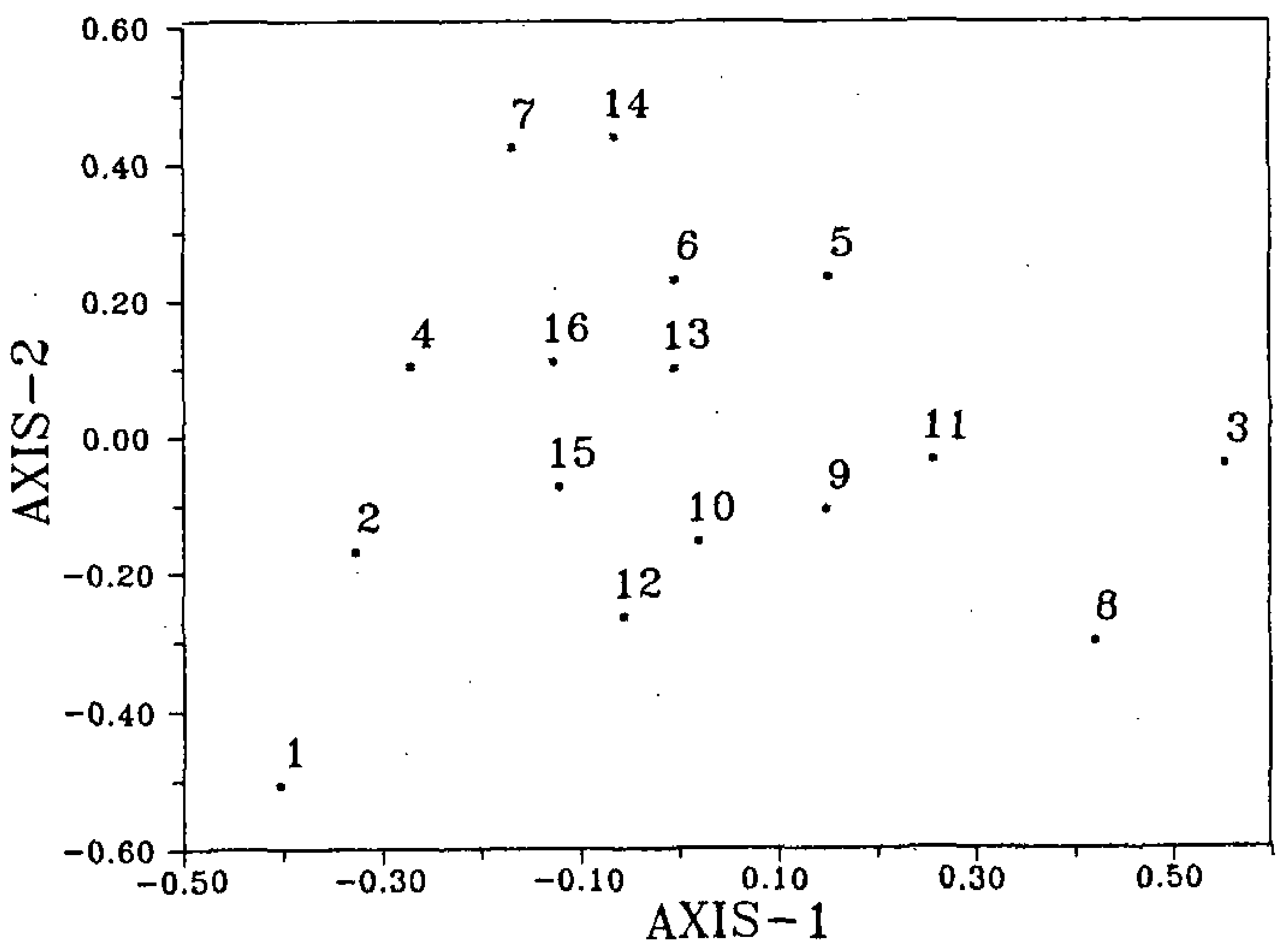

Figure 2. Distribution of 16 species of dung beetles based on their interspecific distances. The two axes derived by Metric Multidimensional Scaling analysis of the interspecific distances together account for 72% of the variance (Axis-1 : 60.80% and Axis-2: 11.10%).

between communities might occur because AI weighs the biological heterogeneity of the community as well as the evenness of the species.

It is also possible to estimate relative contributions of each of the species to the total diversity in AI and accordingly estimate biodiversity value of the species in the community. This can be given by

$$R(i) = \sum_{j=1}^{n} (P_i d_{ij} P_j) / \mathrm{AI}. \qquad (3)$$

Note that the $R(i)$ increases both with the frequency (how common it is) and with the distance of the species with others. Such an estimate of contribution will be highly useful in evaluating the cost of losing that species to the total community diversity and also probably to the ecosystem as a whole. Though this might be possible with other indices also, their assumption of equality of species does not justify the estimated importance of the species. We have estimated the relative contribution of the 16 species to AI for the pooled data of dung beetles and plotted these against their frequencies (Figure 1). In Figure 1, all those species that are relatively distant (different) from others fall above the line while those that are relatively similar to others are expected to fall below the line. The Metric Multidimensional Scaling analysis[7] using the distance matrix (Table 4) shows that species numbered 1, 8 and 3 are placed far away from the rest based on their distance to the rest of the species (Figure 2). Accordingly, though *Onthophagus truncaticornis* (No. 15 in Figure 1) contributes highly through its frequency compared to *Caccobius meridionalis*, (No. 1 in Figure 1) it is biologically more similar to other species (average distance to other species is 4.21; Table 4; Figure 2) compared to the latter (average distance is 6.43; Table 4). Consequently they contribute almost equally to AI. Similarly, *Onitis philemon* (No. 8; Figure 1 inset) falls above the line compared to *Onthophagus rectecornutus* (No. 12), suggesting that it contributes substantially to AI despite its low frequency. In fact *O. philemon* is biologically very distant to other species (average distance is 6.52; Table 4; Figure 2) compared to the latter (average distance is 4.04; Table 4; Figure 2).

We recognize two problems with the proposed index the way it is conceived. First, it presupposes that all the attributes combined to arrive at a distance are equally important, which might not be true because of the probable differences among the variances of the traits. Nevertheless, we have computed the z-scores for all the quantitative traits which might partly resolve this problem. However, the computation of the distance does not account for the correlations that might exist among the traits. This could probably be addressed by the use of a suitable multivariate distance measure.

Second, the proposed index is constrained by the extent of the biological information available on species. In the absence of such information, AI could only be computed based on taxonomic differences. Since taxonomic distance is likely to be correlated with other distances such as morphometric and functional, the AI based purely on taxonomic distances could well serve the purpose. When AI is thus computed purely on taxonomic distance, it is also possible to include the species across systematic groups and in this sense AI permits computation of diversity across any range of taxonomic groups from microbes to mammals by extending the taxon hierarchy to orders, classes, phyla and kingdoms. Thus unlike other indices, AI integrates biological information of species and informs '...how different the inhabitants are from each other', within a community[1].

Appendix I. Relative abundances of 16 dung beetle species encountered in cattle dung pats sampled in different sites around Bangalore between 19 October and 6 March 1997

		Number of individuals												
		Samples												
	Species	1	2	3	4	5	6	7	8	9	10	11	12	Total
1.	*Caccobius meridionalis*	119	108	1	23	59	2	10	–	3	–	–	14	339
2.	*Caccobius unicornis*	23	2	–	–	–	–	–	–	–	–	–	–	25
3.	*Copris indicus*	7	7	–	1	–	–	–	1	–	–	–	–	16
4.	*Drepanocerus setosus*	8	12	21	4	2	2	–	7	–	2	–	4	62
5.	*Liatongus rhadamistus*	1	3	–	–	–	–	–	–	–	–	2	–	6
6.	*Oniticellus cinctus*	–	8	–	3	33	1	–	22	1	–	26	2	96
7.	*Oniticellus spinipes*	–	–	–	–	1	2	1	–	–	–	–	3	7
8.	*Onitis philemon*	10	28	12	18	2	–	–	–	–	–	–	–	70
9.	*Onthophagus catta*	4	–	–	1	–	–	–	–	–	–	–	–	5
10.	*Onthophagus dama*	3	2	3	17	33	1	3	–	1	–	–	–	63
11.	*Onthophagus pactolus*	–	2	–	–	–	–	–	–	–	–	–	–	2
12.	*Onthophagus rectecornutus*	4	6	8	1	3	7	4	48	4	9	20	41	155
13.	*Onthophagus spinifex*	1	1	–	–	–	–	–	–	–	–	–	–	2
14.	*Onthophagus tarandus*	6	–	–	1	–	–	–	–	–	–	–	–	7
15.	*Onthophagus truncaticornis*	11	8	86	25	13	135	101	186	169	124	11	28	897
16.	*Sisyphus* sp.	2	–	–	–	–	–	–	–	–	–	–	–	2
	Number of pats/sample	17	8	11	9	17	10	10	10	10	10	10	10	132
	Total species	13	12	6	10	8	7	5	5	5	3	4	6	16
	Total individuals	199	187	131	94	146	150	119	264	178	135	59	92	1754

Appendix II

Morphological traits

Length and breadth of the head
Length and breadth of the thorax
Length and breadth of the elytra
Presence or absence of cephalic horns at four positions of the head (0/1)*
Number of cephalic horns
Presence or absence of thoracic horns(0/1)*
Number of thoracic horns
Height of the thorax
Height of the abdomen
Number of spines on fore tibia

Functional traits

Colonization stage: fresh (1), old (2) or very old dung (3)*
Breeding habits: burrowers (1), tunnelers (2) and rollers (3)*
Duration of association with dung pat from the time of colonization: short (1), medium (2) and late (3)*
Number of dung types exploited by each species of beetle.

* Qualitative traits.

1. Harper J. L. and Hawksworth., D. L., *Proc. R. Soc. London*, 1994, **B345**, 5–12.
2. Gaston, K. J., in *Biodiversity: A Biology of Numbers and Difference* (ed. Gaston, K. J.), Blackwell Science, London, 1996, pp. 77–113.
3. Magurran, A. E., *Ecological Diversity and Its Measurement*, Croom Helm, London, 1988, pp 1–179.
4. Williams, P. H. and Humphries, C. J., in *Biodiversity: A Biology of Numbers and Difference* (ed. Gaston, K. J.), Blackwell Science, London, 1996, pp. 54–76.
5. May, R. M., *Proc. R. Soc. London*, 1994, **B345**, 13–19.
6. Named after the 'Avalanche Meetings' organized by 'Tuesday Group', UAS, Bangalore. During one such meeting, 'Biodiversity: Conceptual and empirical issues' held during Feb. 1997, the need for a measure of diversity that accounts for biological heterogeneity of the sample was felt and this index was developed.
7. Colgon P. W. (ed.), *Quantitative Ethology*, John Wiley and Sons, New York, 1978.

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