

A COMPARATIVE STUDY OF THE STATISTICAL BEHAVIOUR OF DIVERSITY AND EQUITABILITY INDICES WITH REFERENCE TO DESERT VEGETATION

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Abstract

In a moderately diverse desert vegetation, diversity is almost equally well measured by McIntosh's $1 - \frac{\sqrt{\sum n_i^2}}{N}$ and Margalef's \bar{H} . McIntosh's index $\frac{N - \sqrt{\sum n_i^2}}{N - \sqrt{N}}$ show a somewhat low variability. The equitability is best measured by $\frac{N - \sqrt{\sum n_i^2} - [N - \sqrt{[N - (S-1)]^2 + (S-1)}]}{N - \frac{N}{\sqrt{S}} - [N - \sqrt{[N - (S-1)]^2 + (S-1)}}$ though $\frac{N - \sqrt{\sum n_i^2}}{N - \sqrt{[N - (S-1)]^2 + (S-1)}}$ appears to be substantially more advantageous than other currently used equitability indices. Equitability indices were insensitive to small sampling variability and ordinary standard deviation was found to be appropriate equitability measure in situation where relative abundance pattern was geometric or approximately geometric. The two indices of species richness (S/\sqrt{N} and $S-1/\log N$) show similar statistical behaviour.

Introduction

Diversity is one of the major parameters to describe a community and it has often been related to various community attributes viz., productivity Auclair *et al*, 1967), structure Glenn-Lewin, 1975; Shaukat *et al*, 1976), dynamics Reiners *et al*, 1971), stability (Johnson, *et al*, 1975), niche structure (Johnson, 1977), evolution Whittaker, 1972), environmental factors, gradients and environmental predictability Auclair *et al*, 1976). Comparisons of habitats in time or between habitats of communities are frequently made but the statistical behaviour of diversity and equitability measures and their statistical significance is seldom observed. The statistical behaviour of diversity and equitability measures has been studied by Hiep & Engels (1974) in a low diversity community of meiobenthic copepods of shallow brackish water (mean number of species = 4.09 ± 0.1150). The present paper describes the distributions of some common diversity measures and their evenness components in a moderately diverse desert herb vegetation of southern Sind to evaluate the suitability of diversity and equitability measures for the

desert vegetation. Since the use of equitability indices has been severely criticized (Whittaker, 1972; Peet, 1974, 1975), the sensitivity and applicability of these indices was also evaluated.

The statistical behaviour is studied in relation to desert herb vegetation as relatively few studies on diversity relations have been conducted with reference to desert communities, though substantial attention has been paid to analyse diversity patterns of forests, grasslands or phytoplankton communities (Whittaker, 1975).

Material and Methods

Thirty stands of desert herb vegetation situated in the vicinity of Karachi, southern Sind, were sampled by twenty 1 m² randomly placed quadrats in each. The stands selected for sampling were as far as possible visually homogeneous and free from any major disturbance whether physical or biological.

For each sample, diversity and equitability were calculated by various common diversity and equitability indices (Margalef, 1957; Simpson, 1949; McIntosh, 1967; Shannon & Weaver, 1949; Pielou, 1969; Hurlburt, 1971; Sheldon, 1969; Heip, 1974) and the frequency distributions obtained were characterized by their mean (\bar{X}), standard deviation (s) and coefficient of variation ($-\frac{s}{\bar{X}} \times 100$) and tested for normality by calculating skewness (g_1) and kurtosis (g_2) utilizing K-statistic (Fisher, 1948).

The importance value curves (Whittaker, 1975) for 11 samples representative of low, intermediate and (relatively) high diversity (\bar{H}) are presented to portray the underlying relative abundance pattern of the desert communities and for the purpose of comparison with the quantum of species diversity.

The sensitivity of commonly used equitability indices to small sampling variation was evaluated with the aid of a hypothetical example (Table 2) simulating the structure of desert plant communities. In vegetational sample of size $N = 294$ the species of one individual was changed in rare, most abundant and species of intermediate importance. Equitability of these samples was computed in accordance with the commonly used equitability indices to observe their response to small sampling variation (Peet, 1974).

The mechanical validity of equitability indices was verified with respect to another line of argument. Since equitability is the evenness of allotment of individuals among the species, it implies that as the importance value of species in a sample approaches equality the standard deviation of the importance value should approach zero. Alternatively, as the quantum of importance value becomes more uneven, the standard deviation should increase. Thus, a significant inverse relationship between standard deviation and an equitability index should indicate the ability of the index to quantify the evenness component of diversity. Hypothetical data on 10 small samples where the importance distribution was geometric or approximately geometric was employed. Standard deviation (s) of these samples were computed and correlated with equitability values for the samples.

Results

a) Statistical behaviour of diversity and equitability indices.

The sample statistics calculated for various diversity and equitability measures of the 30 stands are given in Table 1 and the relative abundance pattern of some representative stands, are portrayed by means of dominance diversity curves in Fig. 1.

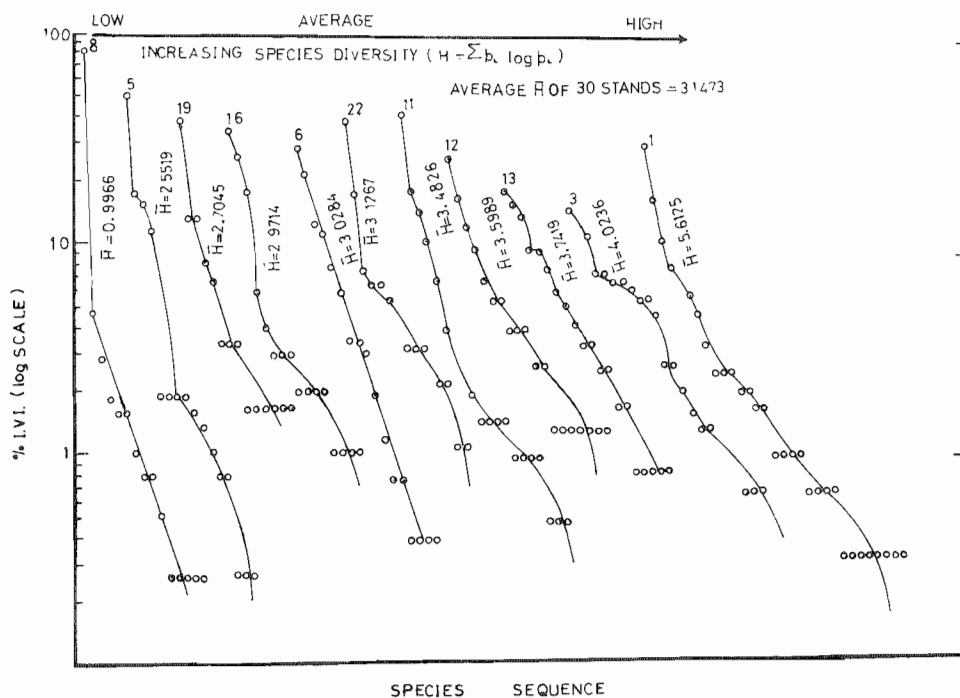


Fig. 1. Dominance-diversity curves for 11 desert herb communities (see text for explanation).

The importance value curves (Fig. 1) for the stands (except stands 2 and 1) are essentially linear on the semilog plot, indicating geometric distribution of species abundance. However, stands 1 and 3 that have high diversity, exhibit an abundance pattern approaching lognormal distribution. Mean density of herbs in the stands was 19.096 ± 2.064 (number/m²), the mean number of species was 18.5 ± 0.68 and total number of species being 98.

Certain conclusions on the suitability of diversity measures and their evenness components for the desert herb vegetation of Sind can be drawn with the help of Table 1. Among the indices of general diversity D and \bar{H} show relatively low variability, significant negative kurtosis ($p < 0.001$) but non-significant skewness. McIntosh's diversity indices

Table 1. Diversity-indices (richness, general diversity and equitability), their mean, dispersion and distribution statistics.

| Diversity Index | Author | \bar{X} | S | C.V. % | s_1 | s_2 |
|---|---|-----------|--------|--------|--------------------|------------|
| $d = \frac{S-1}{\log N}$ | Margalef. (1957) | 8.055 | 1.749 | 21.721 | +0.00658 (n.s.) | -3.6156*** |
| $d = \frac{S}{\sqrt{N}}$ | Menhinick. (1964) | 1.462 | 0.394 | 26.965 | +0.0037 (n.s.) | +3.7194*** |
| S | -- | 18.5 | 3.748 | 20.262 | +1.202549* | +2.8566*** |
| $\bar{H} = -\sum_{i=1}^s p_i \times \log_2 p_i$ | Shannon and Weaver (1949) Margalef (1957) | 3.077 | 0.779 | 25.344 | +0.0039 (n.s.) | -3.4949*** |
| $M_1 = \sqrt{\sum_{i=1}^s n_i^2}$ | McIntosh (1967) | 86.678 | 59.312 | 68.427 | +2.0734*** | +6.5862*** |
| $M_2 = N - \sqrt{\sum_{i=1}^s n_i^2}$ | -do- | 101.964 | 48.057 | 47.132 | +0.9884* | +5.6803* |
| $Mc = 1 - \frac{\sum_{i=1}^s n_i^2}{N}$ | -do- Heip & Engels (1974) | 0.543 | 0.128 | 23.68 | +0.2862 (n.s.) | +1.9466* |
| $D = 1 - \frac{\sum_{i=1}^s p_i^2}{N}$ | Simpson (1949) | 0.775 | 0.116 | 14.974 | -0.0282 (n.s.) | -3.4608*** |
| $M_3 = N - \sqrt{\sum_{i=1}^s n_i^2}$ | McIntosh (1967) | 0.616 | 0.116 | 18.937 | +0.1759 (n.s.) | +1.9466* |

Table continued.....

| | | | | | |
|---|-------------------------|-------|--------|---------------------|--------------------|
| $M_3 = \frac{N - \sqrt{\sum_{i=1}^s ni^2}}{N - \sqrt{N}}$ (Probits) | 5.0097 | 1.245 | 25.858 | +0.005563 (n.s.) | +0.02732 (n.s.) |
| $M_4 = \frac{N - \sqrt{\sum_{i=1}^s ni^2}}{N - \frac{N}{\sqrt{S}}}$ | 0.735 | 0.130 | 17.752 | +0.1999 (n.s.) | +2.4719** |
| $M_5 = \frac{N - \sqrt{\sum_{i=1}^s ni^2}}{N - \sqrt{[N-(S-1)]^2 + (S-1)}}$ | 6.027 | 2.638 | 43.778 | +0.8276 (n.s.) | +0.7708 (n.s.) |
| $E = \frac{H}{H \text{ max.}}$ | 0.758 | 0.158 | 24.394 | +0.006142 (n.s.) | -4.0634*** |
| $e = \frac{e^H}{S}$ | 1.574 | 1.496 | 95.031 | +0.2874 (n.s.) | -2.8465*** |
| $e' = \frac{H-1}{S-1}$ | 1.613 | 1.535 | 95.128 | +0.02951 (n.s.) | -2.8230*** |
| $V = \frac{[N - \sqrt{\sum_{i=1}^s ni^2}] - [N - \sqrt{[N-(S-1)]^2 + (S-1)}]}{[N - \frac{N}{\sqrt{S}}] - [N - \sqrt{[N-(S-1)]^2 + (S-1)}]}$ | 0.679 | 0.149 | 22.971 | +0.3165 (n.s.) | -0.8327 (n.s.) |
| | McIntosh (1967) | | | | |
| | After DeLong (1975) | | | | |
| | McIntosh (1967) | | | | |
| | -do- | | | | |
| | Pielou (1969) | | | | |
| | Sheldon (1969) | | | | |
| | Heip (1974) | | | | |
| | Hurlbert (1971) | | | | |
| | Johnson et al (1975) | | | | |

* p < 0.05; ** p < 0.01; *** p < 0.001; n.s. = Non-significant; N = Total number of individuals; S = Total number of species; ni = Number of individuals of i th species; pi = $\frac{ni}{N}$; C.V. = $\frac{K_3}{X} \times 100$; Skewness (g_1) = $\frac{K_3}{(K_2)^{3/2}}$; Kurtosis (g_2) = $\frac{K_4}{(K_2)^2}$; $Sg_1 = \sqrt{\frac{6N(N-1)}{(N-2)(N+1)(N+3)}} = 0.42689$; $Sg_2 = \sqrt{\frac{24N(N-1)^2}{(N-3)(N-2)(N+3)(N+5)}} = 0.83274$

$M_1 - M_3$ and Mc exhibit significant positive kurtosis. Skewness being significant for M_1 and M_2 but non-significant for M_3 and Mc . Variability was high for M_1 and M_2 but not for M_3 and Mc .

Of the various equitability indices that of Pielou (E') exhibited low variability but Sheldon's (e) and Hiep (e') yielded extremely high coefficients of variation. The distribution of the last two equitability measures had highly significant negative kurtosis ($p < 0.001$) but non-significant skewness. McIntosh's equitability measures M_4 and V exhibited low variability and essentially symmetrical distribution, M_4 yielded significant positive kurtosis ($p < 0.01$) but V was essentially free from kurtosis. In contrast M_5 exhibited moderate variability and non-significant skewness as well as kurtosis.

The species richness indices d' and d show similar behaviour, both have low variability viz., 26.965% and 21.721%, respectively. They do not depart significantly from a symmetrical distribution but exhibited significant positive and negative kurtosis, respectively ($p < 0.001$).

b) Evaluation of sensitivity and applicability of equitability measures.

The response of 6 equitability indices to very minor change in sample composition is listed in Table 3. The intersample similarity for the 5 samples as calculated by Czeka-howski's coefficient of similarity for all possible combinations ranges from 99.31 to 99.65%. It is evident from Table 3 that all the six equitability indices tested are insensitive to small sampling variations as their values remain almost unchanged, thereby contradicting the finding of Peet (1975).

Fig. 2 gives the hypothetical data on the composition of 10 small samples where

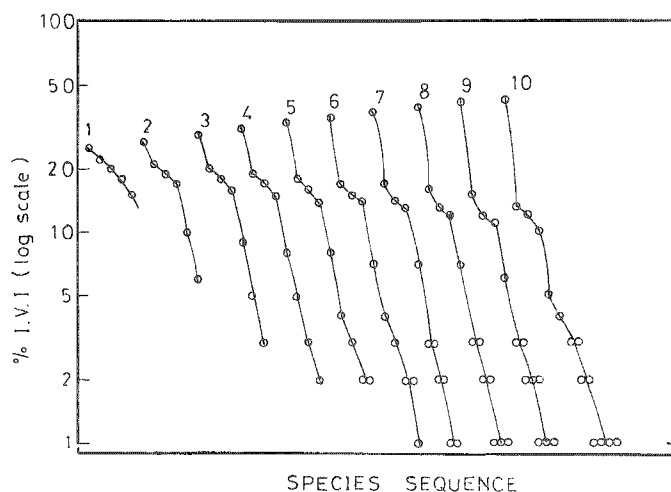


Fig. 2. Dominance-diversity curves for ten hypothetical communities (see text for explanation)

Table 2. Hypothetical data of five communities with fixed S and N but differing slightly in species importance (see text for explanation).

| Species | Communities | | | | |
|---------|--|----|-----|----|----|
| | Number of individuals in ith species (n_i) | | | | |
| | I | II | III | IV | V |
| a | 50 | 50 | 50 | 51 | 50 |
| b | 35 | 35 | 35 | 34 | 35 |
| c | 30 | 30 | 30 | 30 | 30 |
| d | 30 | 30 | 30 | 30 | 30 |
| e | 25 | 25 | 25 | 25 | 25 |
| f | 20 | 20 | 20 | 20 | 20 |
| g | 20 | 20 | 20 | 20 | 20 |
| h | 18 | 18 | 18 | 18 | 19 |
| i | 17 | 17 | 17 | 17 | 16 |
| j | 10 | 10 | 10 | 10 | 10 |
| k | 8 | 8 | 8 | 8 | 8 |
| l | 8 | 8 | 8 | 8 | 8 |
| m | 5 | 4 | 5 | 5 | 5 |
| n | 5 | 6 | 5 | 5 | 5 |
| o | 4 | 4 | 4 | 4 | 4 |
| p | 3 | 3 | 3 | 3 | 3 |
| q | 3 | 3 | 2 | 3 | 3 |
| r | 1 | 1 | 2 | 1 | 1 |
| s | 1 | 1 | 1 | 1 | 1 |
| t | 1 | 1 | 1 | 1 | 1 |

Table 3. Values of equitability as measured by six common equitability indices for the hypothetical data of 5 communities presented in Table 2.

| Community | Equitability measures | | | | | |
|-----------|-----------------------|----------|---------|---------|---------|---------|
| | M_4 | M_5 | V | E' | e | e' |
| I | 0.89915 | 10.82187 | 0.89002 | 0.86499 | 0.15407 | 0.10954 |
| II | 0.89911 | 10.82128 | 0.88996 | 0.86476 | 0.15402 | 0.10949 |
| III | 0.89920 | 10.82247 | 0.89007 | 0.86558 | 0.15418 | 0.10967 |
| IV | 0.89037 | 10.81238 | 0.88916 | 0.86456 | 0.15398 | 0.10945 |
| V | 0.89906 | 10.82069 | 0.88991 | 0.86486 | 0.15404 | 0.10952 |

the importance distribution is geometric or approximately geometric which Whittaker (1965, 1969, 1975) attributes to species poor, environmentally extreme situations e.g.

desert plant communities. Standard deviation (s) of these samples were calculated and correlated with equitability as measured by M_4 , M_5 , V, E' , e and e' . Standard deviation was significantly inversely correlated with all the expressions of equitability. Correlation coefficients (r) and regression equations for these relationships are given below.

$$M_4 = 1.167 - 0.035 s \quad r = -0.873^{***}$$

$$M_5 = 19.887 - 1.306 s \quad r = -0.937^{***}$$

$$V = 1.205 - 0.042 s \quad r = -0.854^{**}$$

$$E' = 1.176 - 0.036 s \quad r = -0.882^{***}$$

$$e = 1.331 - 0.687 s \quad r = -0.895^{***}$$

$$e' = 1.354 - 0.073 s \quad r = -0.889^{***}$$

Discussion and Conclusions

Several diversity indices have been proposed to measure community organization. The statistical behaviour of various diversity measures was compared with reference to moderately diverse desert herb vegetation of southern Sind. The information theory function (\bar{H}) suffered from significant negative kurtosis and has an extremely low variability. On the other hand, McIntosh's indices M_3 and M_5 exhibited significant positive kurtosis ($p < 0.01$ and $p < 0.05$, respectively) and the latter also had low variability. Among McIntosh's equitability indices M_4 and V followed a normal distribution and M_4 had somewhat high variability indicating that it exaggerates the differences in community organization. This drawback was particularly spectacular for Sheldon's (e) and Hiep's (e') equitability measures that had coefficients of variability of 95.03% and 95.12%, respectively.

Therefore, it may be concluded that general diversity can be measured almost equally well by McIntosh's index M_3 and Margalef's \bar{H} , whereas equitability was best measured by McIntosh V though M_5 also has considerable advantage over other equitability measures. The coefficients of variability of M_3 and M_4 are approximately similar and low. The differences in the diversity values yielded by M_3 and M_4 were smaller but these differences can be made more prominent by transforming the diversity values into probits as suggested by DeJong (1975).

Since both the indices of species richness (d and d') have similar statistical behaviour, for the purpose of application one must take into account the practical considerations pertaining to the situation. The index that increases linearly with the increase in sample size in this instance is the one more appropriate. In the present example Menhenick's d' fulfills this criterion and is, therefore, more suitable than Margalef's d.

However, caution must be exercised in extrapolating these results to other communities as these results may be a function of the taxa examined (i.e. their growth form),

of the environment or the total number of species in a community. Furthermore, the extent of uniformity of stands would also have a bearing on the results obtained. These results may be applicable to situations where the relative abundance pattern is geometric or nearly so.

Statistical behaviour, however, is not the only criterion for the suitability of a diversity measure but there are many other theoretical considerations and practical applications that need to be rationally analysed and weighed when one of the several available formulations is to be selected for a given ecological situation (see Whittaker, 1972; Peet, 1974).

Whittaker (1972) has pointed out a number of limitations associated with the measurement of equitability. Firstly, the equitability indices such as E' , e , e' , E and (the latter two were proposed by Lloyd & Ghelardi, 1964) suffer from the fact that they compare a stable with an unstable value (cf. Sheldon, 1969; Hurlbert, 1971; Whittaker, 1971). Secondly, for standard samples of geometric or lognormal form, these equitability indices are functions of general diversity (\bar{H}) they increase linearly with the increase in \bar{H} and are unable to yield any information on equitability beyond that expressed in \bar{H} . Thirdly, with the disparity in sample size for given importance distribution (Whittaker, 1965) equitability varies, but the interpretation of the variation in equitability would be erroneous. Whittaker (1972, 1975) opined that \bar{H} itself is the best measure of equitability. Recently, Peet (1975) demonstrated that the indices of equitability suffer from certain mathematically undesirable properties, no matter whether the maximal diversity is limited by the number of species or by the number of individuals (N). Using hypothetical data pertaining to two populations A and B with N equal to 1000, Peet (1975) showed that minute sampling variation such as changing the species of one individual in a sample of 1000 could easily sway the results in one direction or the other. All of the 14 indices of equitability tested were found to be extremely sensitive to sampling variability. If the indices are to be meaningful they should be relatively insensitive to such a variability. The implication, according to Peet, is that "at best ecologists may have lost a fair amount of time calculating relatively meaningless numbers". The evidence provided by Peet, however, does not appear to be fully convincing, because: (a) the sample of 1000 is large for many plant communities e.g. desert communities. (b) community A consists of 3 species and community B of 4 species in samples of 1000. Thus the number of species are relatively very low for a large sample of 1000. However, when the sensitivity of equitability indices was tested with reference to a hypothetical example, closely resembling the dominance-diversity pattern in desert plant communities, the equitability measures were found to be insensitive to minor sampling variation. Thus we are led to conclude that equitability indices are useful at least in relation to desert plant communities. A significant inverse relationship between standard deviation and an equitability index observed in the present study indicates the ability of equitability indices to quantify the evenness component of diversity. In fact, Fager (1972) has suggested an equitability measure based on standard deviation of importance value and Peet (1974) suggests that in situations of lognormal distribution the logarithmic standard deviation provides one of the most intuitively appealing measure of equitability. Apparently, the ordinary

standard deviation is an appropriate equitability measure when the relative abundance pattern is geometric.

It is not yet clear what the ecological implications are of high and low equitability. However, some theoretical stabs in this direction have been made by Emlen (1973). A high equitability may result in highly stable environment over a prolonged period of time. For instance, the increasing species diversity (H') of benthic foraminiferans found with increasing ocean depth by Buzas & Gibson (1969) was predominately attributable to increasing species richness at shallow depths but in deep water (increasingly old, stable communities) was due primarily to an increase in equitability. Similar conclusions are drawn by Kricher (1972) in his study of bird species diversity of three seral stages, representative of old field succession on the New Jersey Piedmont.

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