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RELATIVE DIVERSITY INDICES¹

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Abstract. Diversity indices are frequently applied in the form of ratios of absolute diversity to the maximum diversity possible. Regardless of whether the maximum diversity is defined to be limited by the number of species or by the number of individuals present, the resultant indices can be shown to possess mathematically undesirable qualities. All such indices, including equitability as measured by Pielou's J and J' , Lloyd and Ghelardi's ratios, redundancy, and the scaled diversity formulations of Fager, are inappropriate for most ecological applications.

Key words: Brillouin formula; diversity indices; equitability; evenness; information theory; redundancy; Shannon formula.

INTRODUCTION

Numerous diversity concepts exist in the ecological literature. One of the most frequently applied combines species richness or number with equitability, or the evenness with which individuals are distributed among species. Examples of indices proposed to measure this concept include those of Simpson (1949), Shannon and Weaver (1949), Brillouin (1956), McIntosh (1967), and Hurlbert (1971). Such diversity indices can be scaled in numerous ways. The object of this paper is to illustrate important but frequently overlooked limitations in the use of relativized forms of these and related indices.

SCALING WITH A VARIABLE SPECIES NUMBER

Consider the effect of scaling diversity relative to the maximum diversity possible when no restriction is placed on species number. This maximum will occur when each individual belongs to a different species. Applying this approach to information theory, Shannon and Weaver (1949) used the term "relative information." Only Margalef (1958) and Kohn (1968) have applied this definition of relative information to ecological diversity, although Colwell and Futuyma (1971) have used a similar formulation as part of a niche breadth index. More recently, Hendrickson and Ehrlich (1971) have suggested that all diversity indices can be scaled in such a manner.

Now consider the application of this approach to the information theory statistics. The information content of a sample can be measured by means of the Brillouin formula: $H = (1/N) \log (N!/\prod N_i!)$ where N_i is the number of individuals in the i th species and N is the total number of individuals. An alternative measure, the Shannon formula, is fre-

quently preferred: $H' = -\sum P_i \log P_i$ where P_i is the percentage of the individuals represented by species i and is estimated by N_i/N . Since the maximum diversity possible for N individuals occurs when each individual belongs to a different species (i.e., $P_i = 1/N$ for each species), the maximum value for the Shannon index is $\log N$ while the maximum for the Brillouin index is $(\log N!)/N$. Thus, relative information can be calculated either as

$$H_R = [\log (N!/\prod N_i!)] \div \log N!$$

or as

$$H'_R = [-\sum P_i \log P_i] \div \log N.$$

An important question concerns the response of diversity indices when applied to a hypothetical community with an infinite number of individuals but with the number of species and their relative abundance predetermined. Such a population approximates sampling randomly from a well-defined universe. The Shannon index is based on percentage composition by species. Consequently, under these conditions and with increasing sample size, the index approaches a constant value, as do related diversity indices such as those of Simpson (1949) and McIntosh (1967). For an infinite sample size the Brillouin index approaches the Shannon index (using the Stirling approximation for $\log N!$), so it too approaches a constant value under these conditions.

Given that the Brillouin index (H) approaches a constant with increasing sample size, then the relativized Brillouin index (H_R), which has a sample size term in the denominator, must decrease with increasing sample size. To illustrate, let $\log (N!/\prod N_i!) = Q$. Then $H_R = Q/\log N!$, while H is merely Q/N . Since $N \neq c \log N!$, for all N where c equals a constant, the two indices must diverge with increasing N . The same results can be obtained for the relativized Shannon index using N and $N \log N$ as the divisors of Q .

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TABLE 1. Equitability values for two similar samples

Index ^a	Population A ($N_i = 500,300,200$)	Population B ($N_i = 500,299,200,1$)
$V'(H')$ (Pielou's J' , 1966)	0.937	0.750
$V'(H)$ (Pielou's J , 1966)	0.937	0.747
V' (Simpson)	0.930	0.827
V' (McIntosh)	0.907	0.768
$V'(H')$	0.936	0.744
$V(H)$ (Margalef 1958)	0.936	0.744
V (Simpson)	0.930	0.827
V (McIntosh)	0.907	0.767
Redundancy (Patten 1962)	0.064	0.254
Variance index (Peet 1971)	0.930	0.827
SD (Fager 1972)	0.735	0.583
Number of moves (Fager 1972)	0.699	0.466
$\exp(H')/S$ (Buzas and Gibson 1969)	0.933	0.705
H/M (Lloyd and Ghelardi 1964) ^b	0.344	0.272

^a V and V' notation follows Hurlbert (1971); text gives details.

^b Lloyd and Ghelardi's alternative formulation of S'/S produces similar results. (Here M refers to the value of H obtained by assuming a MacArthur model for the same number of species, and S' refers to the number of species distributed according to a MacArthur model which would produce the same value of H .)

The failure of relativized diversity indices to approach constant values with infinite sample size strongly suggests that such indices are inappropriate for most studies of ecological diversity. Only under conditions of identical sample size are two populations strictly comparable by these measures. This property can be shown to hold for all diversity indices relativized in an analogous manner.

SCALING WITH A FIXED SPECIES NUMBER

The second class of indices to be considered represents attempts to measure the evenness or equitability component of diversity independently from species richness. Fourteen specific indices are used as examples of this group. Most of these indices relate a diversity index to the maximum value the index can attain, given that the number of species is fixed. This can be achieved in two ways which converge for large sample sizes: evenness = D/D_{\max} and evenness = $(D - D_{\min})/(D_{\max} - D_{\min})$ where D_{\min} and D_{\max} refer to the minimum and maximum values, respectively, that a diversity index D can attain. Hurlbert (1971) has referred to these as V' and V respectively. The first nine indices considered are of this or a closely related form. Included are the indices of Simpson, McIntosh, Shannon, and Brillouin relativized by computing both V and V' , plus the redundancy measure of Patten (1962)

(redundancy = $1 - V(H')$ or $1 - V(H)$). The most widely used of the nine are Pielou's (1966, 1967) J and J' which are equivalent to $V'(H)$ and $V'(H')$, respectively. The remaining five indices include Fager's (1972) number of moves and standard deviation indices, Peet's (1971, see Whittaker 1972) variance index, Buzas and Gibson's (1969) $\exp(H')/S$ (where S refers to species number and H' is calculated using natural logarithms), and Lloyd and Ghelardi's ratios (1964).

All these indices contain a term S for species number; they are therefore sample size dependent. Pielou (1966) justified her J index by noting that S does not refer to the number of species in the sample but to the number in the universe, the number of species which would be in the sample if it were complete. For most biological populations this number is impossible to determine. The result has been that most workers wishing to measure equitability have selected one of these indices and substituted the number of species in the sample for the number in the universe. In consequence, (1) the results are biased in that they consistently overestimate evenness, and (2) differences in species number resulting from sample size or stochastic variation can greatly affect the result. Of these, (2) is more significant. A bias does not prevent some underlying patterns from being discerned, whereas high sensitivity to sample variation can completely mask the useful information.

An example illustrates the sensitivity to small sampling variation which results from substituting the sample species number for the number of species in the universe. Table 1 lists the responses of the 14 evenness indices to a very minor change in sample composition. The species of one individual in a sample of 1,000 has been changed. Sampling error could easily sway the result one direction or the other, so if the indices are to be meaningful they should be relatively insensitive to such a change. Table 1 shows all the indices to be highly sensitive to this small change. The implication is that at best ecologists may have lost a fair amount of time calculating relatively meaningless numbers.

These results bear also on Fager's (1972) recommendation that all diversity measures be relativized. Fager seems not to have recognized that such scaling does not decrease, but much increases, the effect of sample size on the measurement. In general, diversity indices should not be relativized. Several years ago Sheldon (1969) suggested a similar conclusion in a comparison of three equitability indices. Nonetheless, scaled diversity indices have continued to be used and several new ones have been proposed. It is hoped that the present proliferation of indices will soon end and that in the future more careful

testing of indices by authors, reviewers, and users will precede publication and application.

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