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Note on biological diversity, evenness, and homogeneity measures

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Summary. This paper is concerned with the measurement of diversity of a biological or ecological sample of individuals belonging to various species. Using the concept of statistical odds, an alternative diversity measure with an appealing interpretation is formulated as a simple modification of the popular Simpson index. If $\sum p_i^2$ denotes the sum of the squared proportions of individuals belonging to the different species in the sample, the new odds measure of diversity is simply defined by $OD = (\sum p_i^2)^{-1} - 1$ and has the following interpretation: OD is the odds that two individuals selected at random (with replacement) from the sample are of different species. The same modification is also applied to a couple of other measures in use, providing them with convenient odds interpretations. These measures are all members of the same parameterized family, which represents a slight modification of the Hill's family. The inverse of OD is proposed as an odds measure of species homogeneity. Also, some properties of the different measures are outlined, and the measurement of evenness is discussed. Finally, some new indices of individual species dominance and surprise are briefly mentioned.

Whenever an investigator is analyzing one or more samples of species from some population(s), the ecological diversity or species diversity may be one of the characteristics of interest. Although various definitions have been offered as to what is meant by diversity, there seems to be general agreement that the diversity of a biological system depends on the number of species present and the nature of the distribution of individuals over the species. Numerous measures of diversity have been proposed in the ecological literature, a most extensive review of which has been provided by Washington (1984).

It would seem appropriate to require that an acceptable measure of diversity should at least (a) be reasonably simple to compute and understand, (b) have some appropriate foundation in terms of a biological theory, statistics or mathematics, (c) be influenced by both the number of species and the degree of uniformity or evenness of their frequency distribution, (d) have an in-

tuitively reasonable interpretation and (e) possess desirable properties. Some of the proposed measures meet such minimum requirements, but others do not. One diversity measure that is often used, and that obviously fails to meet some of these requirements, is the number of species by itself. A popular measure that satisfies most of the preceding requirements, but one that is not simple to interpret, is the entropy measure (see, e.g., Pielou 1977). The complement of Simpson's (1949) index discussed subsequently meets all of the above requirements. While this diversity index has an appealing statistical interpretation, the reciprocal of Simpson's index, which is one of the most frequently used diversity measures, has no such interpretation.

An objective of the present paper is to propose that, by using the well-known concept of statistical odds, an alternative diversity measure with a nice interpretation may be formulated as a slight modification of the reciprocal of Simpson's index. It also turns out that the same modification applied to other measures being used provides them with meaningful odds interpretations. Some of the properties of the new odds measures, which are members of the same one-parameter family, will be outlined. It will also be suggested that one of these measures is indeed preferable to others. Related measures of evenness and homogeneity will be discussed as will some new measures of relative dominance and surprise for individual species.

Odds measures of diversity

Some of the most popular diversity measures have been formulated as decreasing functions of the *concentration* index $\sum p_i^2$ proposed by Simpson (1949), where p_i is the proportion of individuals (or biomass, etc.) belonging to

the i th species and Σ denotes the summation from $i = 1$ to $i = s$, with s being the number of species in the sample. One such diversity measure is

$$D = 1 - \Sigma p_i^2 \quad (1)$$

which is frequently referred to as the Simpson index, although it could equally appropriately be called the Gini-Simpson index (Gini 1912, see also Good 1982 for some interesting historical comments). Besides possessing a number of interesting mathematical properties (e.g., Bhargava and Uppuluri 1975, Bhargava and Doyle 1974, Patil and Taillie 1982), D also has an intuitively appealing interpretation: it is the probability that two individuals selected at random (with replacement) from the sample will belong to different species.

Rather than D , many researchers seem to prefer the reciprocal form

$$D' = (\Sigma p_i^2)^{-1} \quad (2)$$

(see, e.g., Ludwig and Reynolds 1988, chap. 8, Magurran 1988, chap. 2, 4). This preference seems due to the fact that D' has the familiar *number of species* as its unit of measurement. However, this measure lacks any reasonable statistical interpretation or meaning. For $D' = 12.75$, for example, we know that the reciprocal of the mean (expected) value of the species proportions is 12.75, but this piece of information is of no help to our perception of the species diversity of this particular sample. However, as we shall subsequently demonstrate, by simply subtracting 1 from D' , we get a diversity measure that has clear interpretation in terms of statistical odds. As a formal definition, the odds are given by $o = p/(1-p)$ for a random event whose probability is p . For an event of probability $p = 0.6$, for example, the odds are $o = 1.5$, or equivalently, the odds are 3 to 2 in favor of the event. If $1-p$ is the probability of an event, then the corresponding odds are $p^{-1}-1$. Thus, corresponding to D in (1), with its given probability interpretation, we have the following *odds measure of diversity*:

$$OD = (\Sigma p_i^2)^{-1} - 1 \quad (3)$$

which is the odds that two randomly selected (with replacement) individuals from the sample will be of different species. If the p_i s were to be considered as community (population) probabilities rather than observed sample proportions, then the expression in (3) would be equivalent to an index (Δ_s) briefly mentioned by Hurlbert (1971), and, "If we assume that, in some sense, an individual can compete with himself, then the ratio of interspecific to intraspecific competition is given exactly by Δ_s (p. 580)."

Another diversity measure that can be similarly modified to provide an odds interpretation is the reciprocal of the Berger-Parker index (Berger and Parker 1970).

The Berger-Parker index of species dominance is simply defined as the proportion p_{\max} of the most abundant species. May (1975) concludes that this index is as good as any one-parameter description of species distributions. As a measure of diversity, the reciprocal form p_{\max}^{-1} is usually adopted and is apparently gaining in popularity (Magurran 1988: 41, 76). However, as with D' , the p_{\max}^{-1} suffers from the lack of any meaningful statistical interpretation. This limitation can also be removed by simply subtracting 1 so that we have the measure

$$D4 = p_{\max}^{-1} - 1 \quad (4)$$

which expresses the odds that a randomly selected individual will not belong to the most abundant species.

In terms of the proportion p_{\min} of the least abundant species, the p_{\min}^{-1} has been used in diversity studies (this corresponds to the dimensionless ratio J in May (1975); see also Magurran 1988: 41). Alternatively, we may consider

$$D5 = p_{\min}^{-1} - 1 \quad (5)$$

which gives the odds that a randomly selected individual will not belong to the least abundant species.

We may also point out that the odds measures in (3) – (5) are members of the family

$$N_\alpha = (\Sigma p_i^\alpha)^{1/(1-\alpha)} - 1 = s_\alpha - 1 \quad (6)$$

where α is an arbitrary real-valued parameter and where s_α is the equivalent number of species to be defined subsequently. From this family, which is Hill's (1973) family less 1, we see that OD , $D4$ and $D5$ in (3) – (5) correspond, respectively, to $\alpha = 2$, ∞ and $-\infty$ (i.e., the limits of N_α as α tends to $+\infty$ or $-\infty$).

The *equivalent number of species* s_α in (6), or the *species richness equivalent* $s_\alpha-1$, may be defined as follows. For some real sample of s species, or species richness $s-1$, whose diversity is measured by the middle expression in (6), the species richness equivalent $s_\alpha-1$ is defined as the answer to the question: what is the species richness of a hypothetical and completely even sample having the same diversity as the real sample? Clearly, for $p_i = 1/s_\alpha$ for $i = 1, \dots, s_\alpha$, the middle expression in (6) becomes $s_\alpha-1$ for any value of the parameter α . Of course, for any given real sample of species, s_α depends on α .

Evenness

Another species characteristic that is frequently considered in connection with diversity is the so-called *evenness*, with indices of evenness being basically relative diversity measures or normalizations of diversity mea-

tures. A number of different evenness indices have been proposed in the literature (e.g., Ludwig and Reynolds 1988, chap. 8). Again, none appear to be uniformly preferred. Some of these indices would seem to be quite useless since they are extremely sensitive to the sample size (e.g., Peet 1975).

As examples of evenness indices that depend strongly on the sample size, we mention the entropy index

$$E1 = -\sum p_i \log p_i / \log s \quad (7)$$

considered by Pielou (1977) and the index

$$E2 = [\exp(-\sum p_i \log_e p_i) - 1] / (s - 1) \quad (8)$$

proposed by Heip (1974). We note that $-\sum p_i \log p_i$ is the familiar entropy by Shannon (1948). Clearly, with s being the number of species in the sample, as opposed to the number of species in the community (population), which is rarely known, it is immediately apparent from (7) and (8) that both of these indices are strongly affected by the sample size since so is s . As the sample size is increased, s will tend to increase, but the additional p_i s will be relatively small and so will be the changes in previous p_i s, so that the numerators of $E1$ and $E2$ will remain relatively unchanged whereas their denominators may change substantially. Consequently, and especially if the sample size is not large, a change in sample size may cause the values of $E1$ and $E2$ to change considerably.

As an evenness index that is insensitive to sampling variations, Alatalo (1981) proposed the following measure:

$$E3 = [(\sum p_i^2)^{-1} - 1] / [\exp(-\sum p_i \log_e p_i) - 1] \quad (9)$$

This index differs from that proposed by Hill (1973) because of the -1 term in the numerator and denominator of (9). It is clear from the expression in (9) that $E3$ is quite unaffected by s and hence by sample size since any changes in sample size will have similar and rather minor effects on both the numerator and denominator of $E3$.

As a family of evenness measures that includes $E3$ as a particular case, we may consider

$$E_\alpha = N_\alpha / N_{\alpha-1} \quad (10)$$

where N_α and hence $N_{\alpha-1}$ are defined by (6). For $\alpha = 2$, we see that E_α reduces to $E3$ in (9), that is, $E_2 = E3$. Similarly, $E2$ in (8) is a special case of E_α , with $E_1 = E2$. It is apparent from the definition of E_α that, for any $\alpha \neq 0, 1$, the E_α has similar insensitivity to the sample size as does Alatalo's $E3$. Also, for any α , we have that $0 < E_\alpha \leq 1$, with $E_\alpha = 1$ if and only if $p_1 = \dots = p_s$ and E_α approaching zero as one of the species becomes increasingly dominant. Among the members of the E_α family, we suggest that E_2 is the measure of choice since

it is relatively insensitive to the sample size and, with $\alpha = 2$, the individual p_i s are being reasonably emphasized (weighted) without unduly emphasizing either the most dominant or the most rare species.

Ecological sampling studies are somewhat unique in the sense that the number of species in a community from which the sample is taken is rarely known. In most other situations involving the analysis of categorical data, the number of population categories is known or fixed prior to a sampling study. In such situations, and with s being the number of population categories and OD being the odds measure in (3), the normalized measure $OD/(s-1)$ would be a perfectly appropriate index of evenness. In fact, the $OD/(s-1)$ is the odds measure of qualitative variation for nominal categorical data proposed by Kvålseth (1989, 1991a).

Homogeneity, dominance and surprise

Species homogeneity is a concept whose meaning is opposite that of diversity, or heterogeneity as preferred by Peet (1974). A highly homogenous sample is one with a low level of diversity, that is, a sample in which one or a few species dominate. A sample of low homogeneity is one in which the individuals are fairly evenly distributed over all the species. Thus, the reciprocal of N_α would be a natural generalized measure of homogeneity, that is,

$$H_\alpha = (N_\alpha)^{-1} \quad (11)$$

where N_α is given by (6). For $\alpha = 2$, H_α becomes the odds equivalent of Simpson's (1949) concentration index $\sum p_i^2$, that is,

$$OH = \sum p_i^2 / (1 - \sum p_i^2) \quad (12)$$

where we use OH (instead of H_2) to stand for the *odds measure of homogeneity*. As a convenient interpretation, OH is the odds that two randomly selected (with replacement) individuals belong to the same species. For $\alpha \rightarrow \infty$, we get

$$H_\infty = p_{\max} / (1 - p_{\max}) \quad (13)$$

which is the odds that a randomly selected individual belongs to the most abundant species. If we simply wanted a homogeneity index that is normed to the interval $[0,1]$, we could consider $(s-1-N_\alpha)/(s-1)$. However, this index has no statistical meaning.

The term *dominance* is also frequently used and interchangeably so with the term *homogeneity*. However, besides measuring the overall dominance (homogeneity) of a sample of species, it may also be of interest to assess the extent to which individual species dominate. While the proportionate abundances p_1, \dots, p_s indicate

Table 1. Some properties and interrelationships for three diversity measures and the homogeneity measure.

Characteristic	Diversity			Homogeneity
	<i>OD</i>	<i>D</i>	<i>D'</i>	<i>OH</i>
Formula	$(\sum p_i^2)^{-1} - 1$	$1 - \sum p_i^2$	$(\sum p_i^2)^{-1}$	$\sum p_i^2(1 - \sum p_i^2)$
Interrelations	$OD = D/(1 - D)$	$D = OD/(1 + OD)$	$D' = OD + 1$	$OH = (OD)^{-1}$
Upper Limit ¹	$s - 1$	$1 - s^{-1}$	s	$n^2/(s - 1)(2n - s) - 1$
Lower Limit ²	$(n^2/(s - 1)(2n - s) - 1)^{-1}$	$(s - 1)(2n - s)/n^2$	$(1 - (s - 1)(2n - s)/n^2)^{-1}$	$(s - 1)^{-1}$
Species richness equivalent	<i>OD</i>	<i>OD</i>	<i>OD</i>	$(OD)^{-1}$
Single-species sample	0	0	1	Undefined
Statistical interpretation	Odds	Probability	None	Odds

1. The upper limit of the three diversity measures correspond to a sample of size n for which the proportions $p_i = n_i/n$ are all equal for $i = 1, \dots, s$.
2. The lower limits of the diversity measures correspond to a sample for which $n_i = n - (s - 1)$ for one i and $n_j = 1$ for all $j \neq i$; the lower limits of *OD* and *D* are close to 0 and that of *D'* is close to 1 when the sample size n is large compared to the number of species s .

the extent to which the individual species dominate in an absolute sense, a measure of the *relative dominance* of the i th species needs to be based on a comparison between its sample proportion p_i and the p_j s of the other species in the sample. We suggest that the relative probability measure (r_i) proposed recently by this author (Kvålseth 1991b) may indeed be an appropriate measure of relative dominance. This measure is based on a comparison between p_i and the (weighted) mean (statistical expectation) of all the other p_j s. More specifically, if P_i denotes the distribution of the proportions of all species other than the i th species, then the expected (mean) proportion of the other species is given by

$$E(P_i) = \sum_{j \neq i} (p_j / \sum_{j \neq i} p_j) p_j = \sum_{j \neq i} p_j^2 / (1 - p_i)$$

where $\sum_{j \neq i}$ denotes the summation from $j = 1$ to $j = s$, excluding the $j = i$ term. The ratio between p_i and $E(P_i)$, that is,

$$r_i = p_i / E(P_i) = p_i(1 - p_i) / \sum_{j \neq i} p_j^2 \quad (14)$$

may then serve as an appropriate measure of the relative dominance of the i th species. Accordingly, for the i th species to be considered relatively dominant, it is not sufficient that p_i be large in an absolute sense, but that it be large as compared to the mean of the p_j s for all the other species.

The inverse of r_i in (14) has been proposed by Kvålseth (1991b) as a measure of *surprise* of random events, a concept originally discussed in a statistical sense by Weaver (1948). Within an ecological context, the surprise index $s_i = r_i^{-1}$ may serve to distinguish between rare species (i.e., those with small p_j s) and surprising species (i.e., those with large s_j s). Thus, encountering a rare species is not necessarily a surprising event unless s_i

is large, that is, when p_i is small relative to the mean of the other p_j s. Only when the surprise s_i is much larger than 1 for a species does the ecologist have every reason to be surprised when encountering a member of that species. In terms of statistical odds, we note that $s_i = r_i^{-1}$, with r_i given by (14), has the following interpretation: s_i is the odds that, when two individuals are randomly selected (with replacement) from the sample, both individuals will belong to one species other than the i th species rather than one individual belonging to the i th species.

Discussion

The diversity measure *OD* in (3) has a definite advantage over both *D* and *D'* in (1) and (2). This advantage lies in the fact that *OD* given by

$$OD = (\sum p_i^2)^{-1} - 1 = s_2 - 1 \quad (15)$$

has a direct and meaningful dual interpretation, that is, in terms of odds and species richness equivalent $s_2 - 1$ (i.e., $\alpha = 2$ in (6)). While *D* had a nice probability interpretation, it has to be transformed into *OD* by using $OD = D/(1 - D)$ to obtain the species richness equivalent. In fact, since *D* has limited power of discrimination especially for highly diverse samples (Fager 1972), such transformation of *D* may indeed be warranted. For example, three different samples may have the *D* values 0.95, 0.97, 0.99 whereas the corresponding *OD* values are 19.00, 32.33 and 99.00. The higher discrimination power of *OD* as compared to *D* also follows from a study by Kempton (1979) showing that the degree of discrimination is greater for $(\sum p_i^2)^{-1}$ than for $\sum p_i^2$ (see also Magurran 1988: 71–72). While *OD* and *D'* are equally capable of discriminating between species samples, *D'* has no useful statistical meaning comparable to the odds interpretation of *OD*.

The sample measure OD has similar mathematical properties to those of D and D' since these three measures are monotonic increasing functions of each other. Thus, since the properties of D are well documented in some of the references given previously, we shall only summarize some of the properties and interrelationships between the measures as in Table 1. It may be worthwhile, however, to clarify an important property: that the three measures are increasing functions of both species richness ($s - 1$) and species evenness. This property is apparent from the definitions of the measures and the fact that

$$\Sigma p_i^2 = s^{-1} (2^{-1} \sum_{i=1}^s \sum_{j=1}^s |p_i - p_j|^2 + 1) \quad (16)$$

Thus, since the measures OD , D and D' are decreasing functions of Σp_i^2 , it is clear from (16) that the three diversity measures increase as s increases and as the absolute differences $|p_i - p_j|$ decrease, that is, when the species evenness increases.

A desirable property of any reasonable diversity measure is that it orders species samples according to their so-called intrinsic diversity, that is, it should be Schur-concave (e.g., Kempton 1979, Marshall and Olkin 1979: 410, Patil and Taillie 1982). The OD does possess this property. In fact, any member of the family N_α in (6) has this property for nonnegative values of α . By taking the partial derivatives of N_α with respect to the p_i s we obtain

$$(\partial N_\alpha / \partial p_i - \partial N_\alpha / \partial p_j)(p_i - p_j) = \alpha(1 - \alpha)^{-1} (N_\alpha)^\alpha (p_i^{\alpha-1} - p_j^{\alpha-1})(p_i - p_j) \quad (17)$$

It is apparent that the expression in (17) is less than or equal to zero for all p_i and p_j and all $\alpha \geq 0$, that is, N_α is Schur-concave for $\alpha \geq 0$. Consequently, $OD = N_2$ is Schur-concave. The fact that OD is Schur-concave, and that $OH = (OD)^{-1}$ is therefore Schur-convex, leads to the upper and lower limits of OD and OH given in Table 1.

In conclusion, it would appear that, among the various diversity measures identified in this paper, OD is the measure of choice, perhaps in conjunction with D . Neither D' nor any other member of the family N_α has any important advantage over OD , although $N_0 = s - 1$ and $N_1 + 1 = \exp(-\Sigma p_i \log p_i)$ are frequently used (Magurran 1988). The measures in (4) and (5) corresponding to $\alpha = \pm \infty$ in N_α are appealing because of their extreme simplicity, their main limitation being that they do not fully utilize the information available from the species sample. Thus, we conclude that OD and $OH = (OD)^{-1}$ are indeed appropriate measures of diversity and homogeneity with desirable properties and meaningful interpretations. Finally, we suggest that the relative probability r_i in (14) and the $s_i = r_i^{-1}$ may serve as

interesting and appropriate measures of the relative dominance and surprise of individual species in a sample.

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