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Problems in the measurement of evenness in ecology

Rauno V. Alatalo

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Evenness is considered as the measure of equality of abundances in a community. By comparing artificial abundance distributions the modified Hill's ratio $(N_2-1)/(N_1-1)$ was found to be the most easily interpreted evenness measure. The modification (subtracting 1 from Hill's numbers) is important when species diversity is low. Often the species richness of the community is underestimated, and because of the sampling bias evenness indices not using species richness are recommendable. The most popular evenness index J' seems to be a rather ambiguous measure, since it is for purely mathematical reasons positively correlated with species richness. The ambiguity arises from the logarithmic relation of Shannon's entropy H' to species richness. Hill's numbers with species as units are less ambiguous than diversity measures in general. After all, it is emphasized that there is no single way to measure evenness, and because of the looseness of the concept we have to be cautious in its application.

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Выровненность рассматривается как мера равновесия обилия в сообществе. Путем сравнения искусственного распределения обилия модифицированное отношение Хилла $(N_2-1)/(N_1-1)$ рассматривается как наиболее легко интерпретируемое измерение выровненности. Модификация (вычитаемая 1 из числа Хилла) имеет значение, если разнообразие видов низкое. Часто видовое разнообразие в сообществе недооценивается и, в результате ошибки выборки, рекомендуются индексы выровненности, не учитывающие видовое разнообразие. Наиболее популярный индекс выровненности J' представляет скорее сомнительную величину. т.к. он по чисто математическим причинам коррелирует с разнообразием видов. Неясность возникает из логарифмического отношения энтропии Шэннона H' к видовому разнообразию. Числа Хилла, где вид использован в качестве единицы, менее сомнительны, если разнообразие оценивается в целом. В заключение подчеркивается, что это – не единственный способ оценки выровненности и вследствие слабости этой концепции мы должны быть осторожны в ее использовании.

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Introduction

The use of diversity indices, which combine species richness and evenness of abundance distribution into a single value, has often been criticized owing to the ambiguity of definitions and indices (see Hurlbert 1971, Peet 1974, May 1975). Nevertheless, diversity and evenness indices are often used. Examples of recent studies employing the evenness concept include Austin and Tomoff (1978), Bakelaar and Odum (1978), Reed (1978), Rotenberry (1978) and Järvinen (1979).

The papers of Hill (1973) and Peet (1974) were the first ones to give a firm background to the use of diversity (Peet's heterogeneity) and evenness (Peet's equitability) indices in an unambiguous way, but so far they have been adopted far too rarely. The proliferation of information theoretical, probabilistic etc. indices without any prior tests whether they discriminate communities correctly, has unfortunately been the rule. Many of the papers in the recent book by Grassle et al. (1979) are an exception; Engen (1979) and Taillie (1979) clarify the concept of evenness and its measurement.

In particular, the uncritical use of Shannon's entropy (H'), which is logarithmically related to the number of species, has prevented progress in the application of diversity indices. The statistical properties of this logarithmic measure (see Longuet-Higgins 1971, Webb 1974) have been ignored. Alatalo and Alatalo (1977) showed that by simply using diversity indices which are directly related to species number (e.g. Hill's (1973) numbers, including $\exp H'$) we may get much more interpretable results, when assessing niche or habitat overlap by the components of diversity. The present paper analyzes similar, and other, problems in the measurement of evenness. I shall study the response of evenness measures on artificial abundance distributions to see which indices give the most interpretable results. The emphasis is on the behaviour of indices in practical situations, rather than in their theoretical elegance (see Engen 1979, Kempton 1979).

Measures of evenness

Species diversity can be considered as the measure of the number of species, where each species is weighted by its abundance. Hill (1973) unified such diversity indices into a series, where beginning with N_0 (species richness), through N_1 ($\exp H'$, antilogarithmic Shannon's entropy where $H' = -\sum p_i \ln p_i$) and N_2 ($1/\sum p_i^2$, reciprocal of Simpson's index) and continuing, we get indices, which give less and less weight to the rarest species. In the series, higher numbers thus always give lower diversity values. Figuratively, we may consider N_0 = number of all species, N_1 = number of 'abundant species', and N_2 = number of 'very abundant' species. The unit of Hill's numbers is *species*, whereas H' , for

instance, is the logarithm of the number of 'abundant' species.

Evenness measures should measure the equality of abundances in the community: maximum evenness (1.0) arising when all species are equally abundant, and the more relative abundances of species differ the lower the evenness is. In accordance with Peterson (1975) evenness is not restricted merely as diversity divided by species richness, but is rather a feature of species-abundance relations independent of any single way of measurement, or any theoretical abundance distribution.

The evenness measures considered are:

- (1) J' (Pielou 1966) is $H'/\ln S$ (S = number of species), or to put it another way $\ln N_1/\ln N_0$. J' is the ratio between Shannon's entropy and the maximum H' , which may arise with a given S . This is so far the most often used measure of evenness.
- (2) $E_{1.0} = N_1/N_0 = \exp H'/S$. This is the ratio of Hill's (1973) numbers corresponding to J' . Hill (1973) proposed that ratios of Hill's numbers may be used as evenness measures, and this ratio had been used already earlier by Sheldon (1969). Figuratively, this is the ratio between the number of abundant species and the number of all species.
- (3) $F_{1.0} = (N_1 - 1)/(N_0 - 1)$. Modification of the former ratio by subtracting from Hill's numbers the minima they can obtain in any community (cf. Hurlbert 1971, Peet 1974).
- (4) $E_{2.1} = N_2/N_1$. Hill's ratio, which has been used by Rotenberry (1978). Peet (1974) proposed the inverse of the ratio (N_1/N_2), which is a measure of unevenness. Though the two ratios discriminate communities in the same order, it is less confusing to consider evenness, which gives values ascending to 1. Figuratively, this is the ratio between the numbers of the very abundant and abundant species.
- (5) $F_{2.1} = (N_2 - 1)/(N_1 - 1)$. The modification as made for $E_{1.0}$ above.

Dependence of J' on species richness

Evenness values should be comparable in communities with markedly different species richness (independent of species number, see Engen 1979). DeBenedictis (1973) showed a purely mathematical positive correlation between J' and species richness or diversity. Secondly, in relation with the correlation, he noted that the variation of evenness tends to decrease with increase in the number of species.

Let us consider a theoretical example, where half of the species are equally abundant and the rest indefinitely rare (Tab. 1). Varying species richness we achieve values of J' over the whole range (0,1), which is quite ambiguous, since in the example evenness may be considered equal or almost equal (see next example) irres-

Tab. 1. Evenness by different indices in theoretical communities where half of the species are equally abundant and the other half indefinitely rare.

Species richness	J'	$E_{1,0}$	$F_{1,0}$	$E_{2,1}$	$F_{2,1}$
2	0.00	0.50	0.00	1.00	1.00
4	0.50	0.50	0.33	1.00	1.00
10	0.70	0.50	0.44	1.00	1.00
50	0.82	0.50	0.49	1.00	1.00
100	0.85	0.50	0.49	1.00	1.00
1000	0.90	0.50	0.50	1.00	1.00

Tab. 2. Evenness for cases when half of the species are represented by five individuals and rest by a single individual.

Species richness	J'	$E_{1,0}$	$F_{1,0}$	$E_{2,1}$	$F_{2,1}$
2	0.65	0.78	0.57	0.88	0.68
6	0.86	0.78	0.74	0.88	0.85
10	0.89	0.78	0.76	0.88	0.87
20	0.92	0.78	0.77	0.88	0.87
100	0.95	0.78	0.77	0.88	0.88
1000	0.96	0.78	0.78	0.88	0.88

pective of species richness. Hill's ratio $E_{1,0}$ is constantly 0.50, as half of the species are abundant.

The modified ratio $F_{1,0}$ approaches 0.50 with increasing species richness, and the reason for the variation is given below. Instead both $E_{2,1}$ and $F_{2,1}$ give maximum evenness in all cases. N_1 and N_2 are insensitive to the indefinitely rare species taking account of abundant species only, and due to the equality of abundances the results given by their ratios are acceptable.

In the other example, which is more likely to arise in nature, half of the species are represented by five individuals and the rest by one individual (or any case where the ratio between the abundant and the less abundant species is 5 to 1) (Tab. 2). The example corresponds to the Lorenz curves analyzed by Taillie (1979). Only the unmodified Hill's ratios remain stable irrespective of species richness, as noted already by Hill (1973) and Taillie (1979). J' rises continuously, and asymptotically approaches 1, which is not to be expected for evenness as all the time half of the species are five times more abundant than the other half. The modified Hill's ratios have an initial rise at low species richness, but soon they converge to unmodified ratios, the asymptotic level being clearly below unity. Taillie (1979) argues that replication should not change the value of evenness, but it is not unreasonable to expect an initial rise in evenness when the number of species is low. Consider the two-species community (5,1) and the four-species community (5,5,1,1). In the former case no two species share the same abundance, whereas in the latter case one species is equally abundant to any

species. With increasing number of species half of the species become equally abundant to any species.

In conclusion, J' seems to converge up to unity as species richness is increased, which is enough to reject the use of J' for comparisons where species richness varies considerably. The increase in J' with increasing species richness is attributable to the logarithmic nature of the indice. Shannon's entropy is logarithmically related to the number of species; 1, 10 and 100 equally abundant species giving H' values 0, 2.30 and 4.60, respectively. The higher the diversity the more species are needed to give the same increase in diversity. Figuratively, J' may be considered as the ratio between the logarithm of the number of abundant species and the logarithm of the number of all species. Assume that both the number of abundant species and the number of all species are doubled in a community. Clearly the ratio between their logarithms (J') will increase at the same time, since it is the difference, not the ratio, of logarithms which remains constant. The doubtfulness of the use of the ratios of logarithmic diversities for evenness estimation has been noted at least by Lloyd and Ghelardi (1964), Whittaker (1972) and Hill (1973). Hill's ratios escape the pitfalls of logarithms, as they are based on Hill's numbers, which have directly species as units.

Sampling bias

Peet (1974, 1975) and Pielou (1977) point out that since species richness is often underestimated with samples of populations (even with large samples), it is difficult to compare large communities with respect to their evennesses (if evenness equation includes species richness). Since species richness is underestimated, evenness tends to be overestimated. The sampling bias is much smaller for Hill's numbers N_1 and N_2 , which are not equally sensitive to the exclusion of the rarest species (see Peet 1974). Peet (1974, 1975) gave an example, which illustrates the marked variation, which may arise due to chance if evenness indices are based on species richness (Tab. 3). Hill's ratios $E_{2,1}$ and $F_{2,1}$, instead give almost the same value for the two samples. Reduced sampling bias is a strong point for the preference of Hill's ratios without N_0 in the measurement of

Tab. 3. Evenness for Peet's (1974, 1975) example.

Sample (numbers of individuals)	J'	$E_{1,0}$	$F_{1,0}$	$E_{2,1}$	$F_{2,1}$
3 species (500, 300, 200)	0.937	0.933	0.900	0.940	0.906
4 species (500, 299, 200, 1)	0.748	0.705	0.606	0.935	0.899

evenness. Furthermore only such Hill's ratios fulfil two relevant properties of evenness proposed by Engen (1979): continuity and non-triviality when $N_0 = \infty$.

Modification of Hill's ratios

Next, I will consider the relevance of the modification for the original ratios of Hill (1973). Peet (1974) noted that as diversity (heterogeneity) decreases, the values of the Hill's numbers and consequently the ratios will converge towards one. Hence a low value of an unmodified ratio could either mean that the overall diversity is low or that the dominance is spread over a number of the more common species in the community.

In the example we have all the possible combinations of abundance relations between two species, diversity being thus very low (Fig. 1). As one species becomes more and more dominant over the other, we should expect that an appropriate evenness measure approaches zero (though in the limiting case of one species in the community evenness cannot be determined). Ambiguously, $E_{2,1}$ has always a fairly high value as postulated by Peet (1974), though he considered the inverse relation and had consequently low values of evenness. Instead, the modified ratios and J' approach zero with increasing dominance of the other species.

Peet (1974) observed another problem with Hill's ratios, when comparing geometric series. The striking feature is illustrated in Tab. 4. In geometric series the parameter k , the pre-emption factor, gives the proportion of the remaining species which belong to the first, second etc. species. The greater the parameter the steeper is the species-dominance curve. With increasing

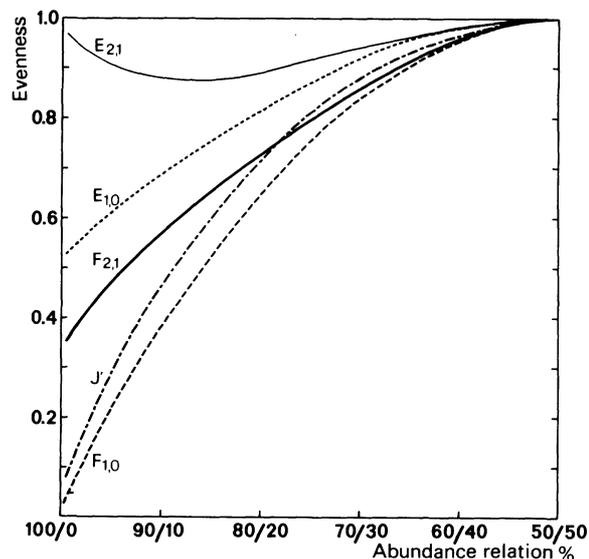


Fig. 1. Evenness for all possible abundance relations in a two species community.

Tab. 4. Hill's ratios for geometric series with different pre-emption factors, k . Diversities calculated according to May's (1975) equations for cases with species richness much larger than one.

Pre-emption factor k	$E_{2,1}$	$F_{2,1}$
0.99	0.964	0.345
0.90	0.852	0.510
0.60	0.760	0.644
0.40	0.743	0.685
0.10	0.736	0.722
0.01	0.736	0.735

evenness, both $E_{2,1}$ and $F_{2,1}$ approach the same value (0.735), but from the opposite directions! The correct, increasing trend with reduced k , is shown by the modified Hill's ratio $F_{2,1}$. When k is near unity, diversities are low and unmodified Hill's ratios high, and the present problem is consequently the same as in the previous example. The modified ratio $F_{2,1}$ also discriminates correctly the three geometric curves (H,F,I) in Peet's (1974) Fig. 4, even though unmodified Hill's ratio $E_{2,1}$ gives ambiguous results. Altogether, the modified ratio $F_{2,1}$ seems to escape the controversies noted by Peet (1974) for the corresponding unmodified Hill's ratio.

Sheldon's example

Sheldon (1969) was perhaps the first to study the response of evenness indices for certain abundance distributions with varying species richness. He considered, for instance, a case where all species except the first are

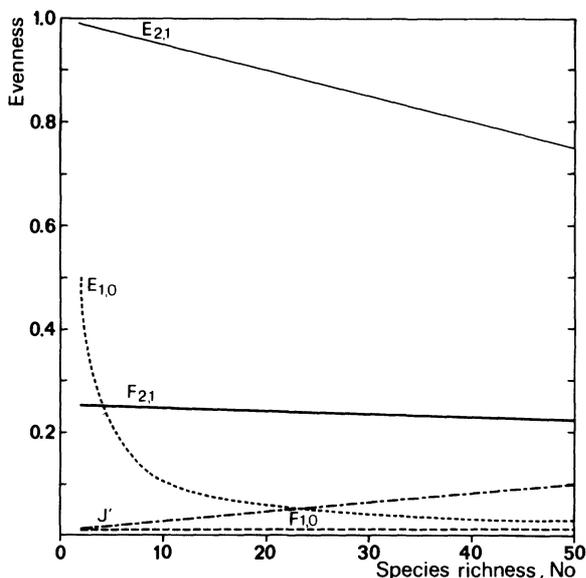


Fig. 2. Evenness for Sheldon's (1969) example, where all species, except the first are represented by one individual in a sample of thousand individuals.

represented by a single individual in a sample of 1000 (Fig. 2). He found J' most appropriate because of its most stable value ($F_{1,0}$, $E_{2,1}$ and $F_{2,1}$ not included). Modified Hill's ratios have even more constant values, $F_{2,1}$ decreasing and $F_{1,0}$ slightly increasing with increasing species richness. Giving weight to the rare species, as with $F_{1,0}$, evenness may be expected to increase as the number of equally abundant rare species increases. Instead with $F_{2,1}$ more weight is given to the abundant species, and decreasing evenness may be expected initially, as there are more and more species that have unequal abundance with the abundant species. When species richness approaches 1000 increased evenness would be expected also in this case, and values of $F_{2,1}$ begin to rise as well. Initially, the unmodified Hill's ratios give much higher values than the corresponding modified ratios, and this controversy at low species richness was already discussed in the previous section.

Theoretical abundance distributions

Theoretical abundance models (e.g. May 1975, Pielou 1977, Engen 1978) provide perhaps the most promising way of studying species-abundance distributions, though it is often difficult to test which, if any, of the models are followed by each community. Hurlbert (1971) noted that among the many possible models probably no one bears any constant relationship to species evenness, and May (1974, 1975) criticized evenness indices (J' , $E_{1,0}$) because they do not discriminate the theoretical abundance distributions included in his comparison, if species richness is low.

MacArthur's (1957) broken-stick model gives rather

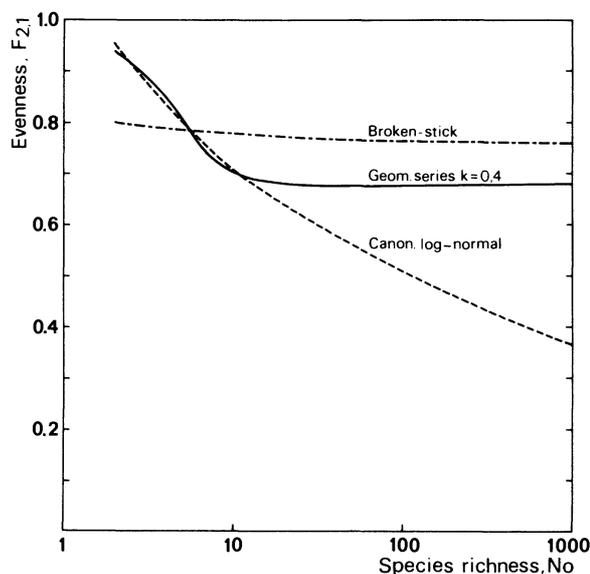


Fig. 3. Evenness $F_{2,1}$ for the broken-stick model, geometric series ($k = 0.4$) and for the canonical log-normal distribution with varying species richness.

even abundances. In geometric series (and logseries) the form of the distribution is steep, and lognormal distribution is intermediate in steepness of the abundance distributions (May 1975). The modified Hill's ratio $F_{2,1}$ is almost constant for the broken-stick model, decreasing from 0.80 to 0.76 with increasing species richness (Fig. 3). If the number of species is less than ten, the $F_{2,1}$ is of the same magnitude for geometric series with $k = 0.4$ and for the canonical lognormal distribution. When species richness is higher, the canonical lognormal distribution gives the lowest $F_{2,1}$, and geometric series intermediate values. The apparent controversy with May's (1975) expectation is explained by the extreme rareness of the rare species in the geometric series; the ten most abundant species making up 99.4% of all the individuals even in large theoretical communities. Since Hill's numbers N_1 and N_2 do not respond at all to the presence of the very rare species, the $F_{2,1}$ is not lowered, even though evenness indices with N_0 as denominator would be low.

None of the evenness indices can be used to test which theoretical abundance model is best realized in any community (May 1975). Pielou (1977) points out that if some theoretical distribution is realized, its parameters are best for considering evenness. But she finds it necessary to have also descriptive statistics that can be used for any community, no matter what the form of its species-abundance distribution and even when no theoretical series can be found to fit the data.

Concluding remarks

The commonly used J' seems to be an ambiguous measure of evenness, as it tends to increase with species richness for purely mathematical reasons. The ambiguity with J' is due to the logarithmical relation of Shannon's entropy to species richness. Alatalo and Alatalo (1980) give some examples of misleading results in ecological studies because of the use of J' . The use of the logarithmic Shannon's entropy H' causes confusion, overcome with $\exp H'$, in other contexts as well (Alatalo and Alatalo 1977). Shannon's entropy may also cause misleading interpretation when we test one of the classic dogmas in community ecology: the increase of community stability with increasing species diversity (or the other way round, cf. May 1973). We might easily count the coefficient of variation of H' in time to measure unstability of the community. But the variation of H' tends to decrease, in any case, with higher diversity because of the logarithmic nature of the measure (see Webb 1974). The decreased coefficient of variation of H' in species rich communities would arise for purely mathematical reasons.

To avoid the pitfalls due to the logarithmic nature of measures, the use of diversity indices with species as units is recommendable, and Hill's (1973) numbers N_1 and N_2 have been recommended by Peet (1974) and Routledge (1979). Furthermore, these indices are

closely related to information theoretical indices (N_1) or probabilistic indices (N_2 , related to *PIE* of Hurlbert (1971), N_2 is the probability of interspecific encounter divided by the probability of intraspecific encounter and this all added by one). In the measurement of evenness, Hill's ratios with the slight modification, seem to be the least ambiguous indices. In particular $F_{2,1}$ seems most interpretable, as we do not need to estimate species richness, which is often very dependent on sample size. Modification of the original Hill's ratios appears important with low species diversity or richness. Different Hill's numbers and their ratios would give indices that weight abundance in a different way, but in most cases N_1 and N_2 suffice to answer any question that these indices can answer (see Peet 1974).

All problems in the measurement of evenness have not been highlighted in the present study, and most likely many problems will never be solved. There is not a single mathematical definition of evenness, which could be shown to be superior to others. Evenness is only loosely defined as the 'equitability of abundances in the community'. We can find an indefinite number of evenness indices, which weight different properties of abundance distributions in a different way. One may ask whether the confusion makes the whole evenness concept useless. But, we find 'loose' indices in other fields of ecology as well (e.g. niche overlap and niche breadth). Even the most useful statistical parameter, the average, can be defined in several ways.

In spite of their popularity, the diversity and evenness concepts have not produced much useful information in ecological studies. One of the reasons for the failure is the uncritical use of various indices, with no knowledge of their response behaviour and of the looseness in the definitions of the concepts. Typically diversity and evenness have been measured as purely descriptive statistics without any reference to important ecological questions or hypotheses. Yet, there are some fields of study, where the concepts, with caution, may be used. Hill's numbers N_1 and N_2 may in some cases substitute the number of species, the estimation of which is often tedious, as the measure of species 'number'. For evenness, one interesting question is: are the abundance relations in communities more equal in predictable than in unpredictable environments, in rigorous than in non-rigorous environments or in unstable than in stable communities (Tramer 1969, Rotenberry 1978, Routledge 1980)?

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