Standardization of species counts – the usefulness of Hurlbert's diversity-index in paleontology.

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Species counts are often used as a measure of diversity in paleontological studies. However, the number of species is not an optimal measure of diversity in a sample, since this entity is normally highly dependent on the number of specimens counted. More species are found in larger samples. The Hurlbert diversity-index provides a means of eliminating differences in sample size, which facilitates comparisons of species counts in samples of widely varying sizes. This index determines the expected number of species (S_m) in a random subsample of m specimens from the total sample. The value of m may be chosen to give greatest weight to either rare or abundant species.
The Hurlbert index was applied to a data-set of benthonic foraminifers from the uppermost Cretaceous of Scandinavia. The sample-sizes in this data-set varied greatly (from 50 to almost 600 specimens), and the number of species (13–65) found in the various samples was closely related to sample size. This relationship did not remain in the standardized species counts (m = 50 in this case), which demonstrates the efficiency of the Hurlbert-index in removing sample-size differences.

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Introduction

Diversity indices are useful measures of the complexity of faunal or floral distributions in paleontological samples. One of the attractive features of diversity indices lies in the reduction of the information provided by the species-distribution in a sample to a single number. A great number of different diversity indices has been described in the literature (see review in Buzas, 1979). Each of these gives different weight to specific properties of the species distribution (richness and evenness of the species). The current status of the field of ecological diversity has been summed up recently in Grassle *et al.* (1979) and Patil & Taillie (1982).

The simplest and most commonly used measure of diversity in paleontology is represented by the number of species found in a sample (for example, Buzas & Gibson, 1969; Douglas, 1973; Balsam & Flessa, 1978; Jørgensen, 1979, Chatziemmanouil, 1982; Srinivasan & Kennett, 1983). Other diversity measures, which also take into account the proportions of the various species, have been employed in paleontological studies of community structure (for example, the Simpson index and the Shannon-Wiener information-index; Ager, 1963; Buzas & Gibson, 1969, Williams & Johnson, 1975; Balsam & Flessa, 1978; Hultberg & Malmgren, 1985). It is well known that these indices are more or less strongly dependent upon the sample-size; thus, the more specimens included in a sample the more species will be found (Kempton, 1979; de Caprariis *et al.*, 1976; Douglas, 1973).

In this communication, we discuss specifically the use of species-counts (number of species) as a diversity index in paleontology, the effects of differences in sample-size on this measure of diversity, and how these effects may be reduced or eliminated. Kempton (1979) gave an example of the inconsistencies which can arise in classifying samples on the basis of species-counts without correcting for sample size. This correction is possible by the use of the diversity-index proposed by Hurlbert (1971). This index, S_m, denoted the "expected species diversity" by Smith & Grassle (1977), permits standardization of species-counts to a common sample-size. Consequently, with this method, it is possible to estimate the number o species (S_m) that one would expect to find in a subsample of m specimens taken at random from a sample of N specimens ($m \leq N$). Smith & Grassle (1977) pointed out that the Hurlbert index satisfies Pielou's (1969) definition of a diversity-measure in that it, for fixed m , is dependent on both the species-richness and the evenness of the proportions of species in a sample. In addition, for large m, it is the only measure described in the literature that is both sensitive to rare species and unbiased (Smith & Grassle, 1977). The estimate of the Simpson index is also unbiased; for $m = 2$, the Hurlbert index is equivalent to Simpson's diversity (Smith and Grassle, 1977).

The Hurlbert index was employed here for a data-set of benthonic foraminifers from the Upper Cretaceous of Scandinavia. Sample sizes varied greatly (from about 50 to nearly 600 specimens), and it was attempted to isolate true intersample-differences in diversity using species-counts by reducing the effect of differences in sample size.

The data-set

Benthonic foraminifers were studied in material from three Scandinavian Upper Maastrichtian localities: Limhamn (southern Sweden), Stevns Klint (eastern Denmark), and Kjølby Gaard (western Danmark). The Limhamn material was collected from four borehole cores (D103, D104, D105, and D106). These cores penetrated between 125 m and 197 m of Upper Maastrichtian chalk. The material from Stevns Klint and Kjølby Gaard was sampled from outcrop sections comprising 10 m and 8 m, respectively, of uppermost Maastrichtian deposits. In all, 80 samples were analyzed, 52 from the Limhamn cores, 15 from Stevns Klint, and 13 from Kjølby Gaard.

Census counts of benthonic foraminifers were made in the larger-than-125 μm fraction of each sample. In all, 167 species of benthonic foraminifers were identified. The census data were prepared by the junior author.

The Hurlbert index

In a sample of N specimens distributed among S species with abundances $N_1, N_2, \ldots, N_s$, $\Sigma N_i = N$, the expected number of species in a random subsample of size m ($m \leq N$) is:

$$S_m = \sum_{i=1}^{S} [1 - C(N-N_i, m) \;/\; C(N, m)],$$ where $C(N-N_i, m) = (N-N_i)! \;/\; [m! \;(N-N_i-m)!]$ and $C(N, m) = N! \;/\; [m! \;(N-m)!]$ for $(N-N_i) \geq m$ and $N \geq m$, respectively, and zero for $(N-N_i) < m$ and $N < m$, respectively (Smith & Grassle, 1977; Kempton & Taylor, 1979).

The value of m is conveniently set at the smallest of the samples in a set of samples. Here, m is put equal to 50, since the sample-sizes range from 51 to 576.

The sampling properties of this index were discussed by Smith & Grassle (1977). They pointed out that this index holds a practical advantage over most other diversity indices in that it permits determinations of minimum-variance unbiased estimators. This estimator of variance may be used to compute approximate confidence intervals for S_m.

It is possible in applications of the Hurlbert index to give particular weight to either rare or abundant species by varying the value of m. For small m, the index is dominated by the abundant species, and the sensitivity to rare species increases with increasing m (Smith & Grassle, 1977). For m =50 (the value used here), the index, therefore, probably relies somewhat on the dominant species. We note that the Hurlbert index has been employed in a study of population structure of deep-sea benthonic foraminifers from the South Atlantic Ocean (DSDP Leg 74; Parker *et al.,* 1984).

Results

Figure 1A shows the relationship between sample-size (N) and number of species (S) in the Limhamn, Stevns Klint, and Kjølby Gaard samples. The number of species is generally greater in the Limhamn and Kjølby Gaard samples than in the Stevns Klint samples. Thus, for any sample-size, more species were found at Limhamn and Kjølby Gaard than at Stevns Klint. As expected, both the Limhamn–Kjølby Gaard and Stevns Klint samples show very clear increases in the number of species with increasing sample-size. The number of species increases from between 13 and 30 for a sample size of about 50 to a maximum of 65 for a sample of 576 specimens.

The standardized number of species (S_{50}) is plotted against sample size in Figure 1B. Whereas the raw species counts (S) were highly dependent on sample size, there is no such obvious correlation in the standardized data. Thus, no major influence of sample-size remains in the standardized species-counts, so the elimination of the differences in sample-size is an effective aid for isolating true differences in diversity among the samples. We also note that the sample-to-sample variation in S is less in Figure 1B so making the discrimination between samples easier. It is significant that the difference between Limhamn–Kjølby Gaard and Stevns Klint is preserved in the transformed species-counts. A larger number of species was noted for a given sample-size at Limhamn–Kjølby Gaard, and these localities also display higher values of S_{50}. The maximum diversity (S_{50}) is also highest at Limhamn – Kjølby Gaard (29 species for two samples of size 105 and 169, respectively, as compared to 22 species for a sample of size 337 at Stevns Klint).

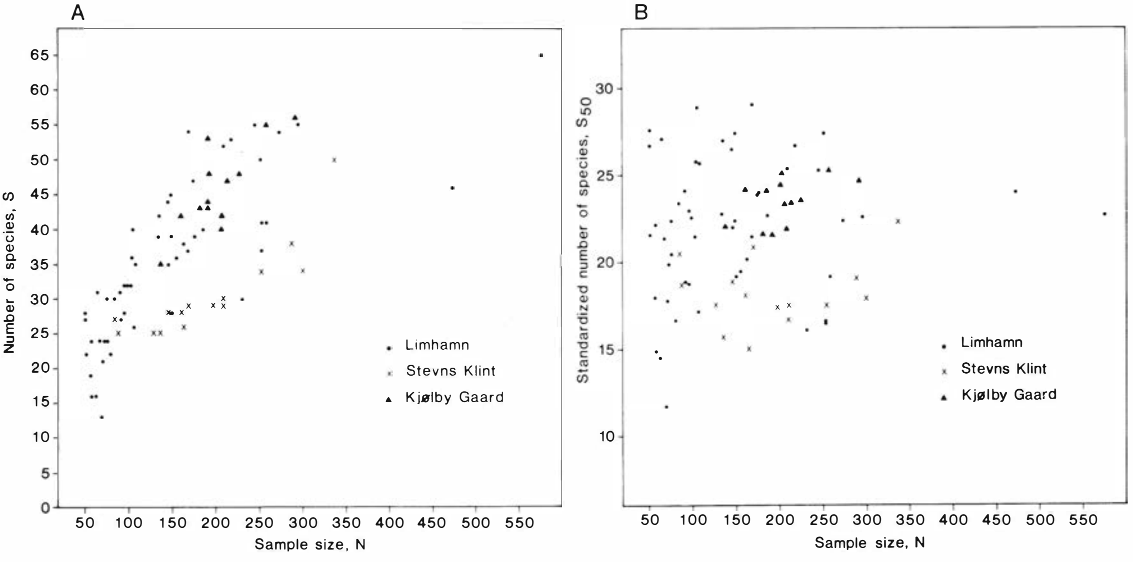

Fig. 1. Relationships between A; sample size (N) and number of species (S) and B; sample size and standardized number of species (S_{50}) in benthonic foraminiferal samples from the uppermost Cretaceous of southern Scandinavia. S (the Hurlbert diversity index) is the expected number of species in a random subsample of m specimens ($m < N$); m is equal to 50 in this study. The number of species (S) increases with increasing sample size, whereas no dependence on sample size exists in the standardized number of species (S_{50}). Note that both the raw and standardized numbers of species are generally greater in the Limhamn and Kjølby Gaard samples as compared to the Stevns Klint samples.

Discussion

Species-counts have been employed frequently as a measure of diversity in paleontological studies. Many workers have noted that this measure is greatly biased in comparisons of samples of greatly differing sizes, but the effect of this does not seem to have been fully realized by some workers. The Hurlbert index provides a simple and straightforward means of reducing the effects of sample-size differences, and should be employed to standardize species-counts whenever the material available in a study does not permit counts of similar sample-sizes.

The following examples demonstrate the change in species-counts accomplished by the standardization procedure. In one of the benthonic foraminiferal samples, consisting of 76 specimens, 30 species were recognized, whereas 55 species were found in another sample of size 295. If the difference in sample-size is not taken into account, one might draw the conclusion that the second sample shows much higher diversity. However, the S_{50} values are similar, 22.4 and 22.6, respectively, indicating that the diversity does not differ between these samples. Similarly, 27 species were found in a sample with N equal to 51 as compared to 46 species in a sample of 473 specimens.The expected number of species in a random subsample of 50 specimens from the second sample is 24.0, whereas S_{50} for the first sample is 26.7. Thus for m = 50, the diversity is in fact higher in the first sample in spite of the many more species found in the second sample.

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