Comparison of different methods for diversity ordering

Tóthmérész, Béla

Ecological Institute, Kossuth L. University, Debrecen, POB 71, H-4010 Hungary; Fax +36 52 431 148;
E-mail TOTHMERB@TIGRIS.KLTE.HU

Abstract. The measurement of diversity, one of the most important concepts in present-day ecology, can be improved by methods of diversity ordering which have recently been developed. This ordering is achieved by a $D(\alpha)$ diversity index family. Indices of this family show varying sensitivities to the rare and abundant species as the scale parameter, α, changes. The aim of this paper is to review and assess 12 methods of diversity ordering and discuss their relationships in detail. Two of the methods are new to the ecological literature.

The diversity ordering methods are compared as to their effectiveness in graphically displaying the differences of community structure and demonstrating the (non-)comparability of communities. Small, medium and large data sets were used to evaluate the methods. A small artificial data set (five to seven species) and a large semi-artificial data set (31 - 141 species) are used in this paper.

The results suggest that Rényi's diversity index family and Logarithmic dominance ordering are the most useful methods for diversity ordering of communities of all sizes. Right-tail-sum diversity ordering performs well for small communities.

Keywords: Diversity family; Diversity profile; One-parameter diversity; Rényi's diversity index.

Introduction: Diversity profiles and their comparison

The diversity concept is of central importance in ecological theory and practice (e.g. Goodman 1975; Grassle et al. 1979; Huston 1979; May 1975). Species richness and diversity are also important in conservation management. They are frequently used as indicators of the 'well-being' of ecological systems (Magurran 1988). Diversity is also widely used in environmental monitoring (e.g. Cairns et al. 1979; Resh 1979; Washington 1984).

There are a great many diversity indices. Their statistical properties have been studied in detail; see the literature cited in Dennis et al. (1979). In practice, however, many researchers have criticized the use of diversity indices in field studies and other applications.

It is well-known that different diversity indices may rank sets of communities in different ways (Hurlbert 1971). Three artificial communities with the following abundances will be used here to demonstrate such differences:

A = (33, 29, 28, 5, 5)   a 5-species community;
B = (42, 30, 10, 8, 5, 5)   a 6-species community;
C = (32, 21, 16, 12, 9, 6, 4)   a 7-species community.

As an example of a difference, A and B are ranked differently by the Shannon (H) and Simpson (D) indices, where the Shannon index is calculated as $H = -\Sigma p_i \ln p_i$, and the Simpson index as $D = 1 - [n_i (n_i - 1)]/[N (N - 1)]$, and here n_i is the abundance and p_i is the relative abundance of the i-th species; $N = \Sigma n_i$. For the two communities the values for H and D are:
$H(A) = 1.3808 < 1.4574 = H(B)$;
$D(A) = 0.7309 > 0.7194 = D(B)$.

Patil & Taillie (1979) emphasized that such inconsistencies are inevitable whenever one attempts to reduce a multidimensional concept to a single number; a community is a multidimensional entity and its diversity is a scalar quantity.

A potential solution is offered by the use of parametric families of diversity indices instead of a diversity index with a numerical value. When we are using a one-parameter family $\{D_\alpha: \alpha \text{ real}\}$ of diversity indices then the family may be portrayed graphically by plotting diversity values D against the (scale) parameter α. This curve, the graph of the $\{D_\alpha: \alpha \text{ real}\}$ family, has frequently been described as the diversity profile of the community (Patil & Taillie 1979, 1982). Essentially, α serves as a scale parameter, and members of the D_α family have varying sensitivities to the occurrence of rare and abundant species as α changes. Diversity profiles play an important role in diversity comparisons. Diversity profiles of the communities A, B and C are presented in Fig. 1 using Rényi's diversity index family.

On the basis of the diversity profiles we can define the diversity ordering of communities in the following way: Community A is more diverse than community B (written as A > B) if the diversity profile of A is above

or equal to the diversity profile of B over the whole range of the scale parameter.

It can be shown that the diversity ordering is a partial order so that if A > B and B > C, then A > C. However, it is not true that for every A and B, either A > B or B > A; i.e. the curves of the two diversity profiles may intersect. In this case the two communities A and B are said to be non-comparable; this means that we can find two diversity indices which order the communities differently. Of course, this situation might reflect important ecological processes which can be interpreted. In Fig. 1, we can see that A and B are non-comparable, and also that community C is the most diverse one: C > A and C > B.

Patil & Taillie (1977, 1979) and Solomon (1979) were among the first to propose the idea of diversity ordering. This idea is important in ecology and has added a new dimension to the ecological approach of diversity. Diversity ordering based on parametric families of diversity indices is not yet frequently used, mainly because these methods involve more calculations than a simple diversity index. Few of these methods are included in any standard computer packages.

Material and Methods

Samples to assess the performance of the methods

The main objective of this paper is to assess the graphical performance of the different methods. Diversity ordering values are compared according to their effectiveness in displaying the differences of community structures. The question is put whether the diversity profiles of different communities are really different, and if they are, how much of this difference is evident from the graphical output of the method. I am also interested in the usefulness of the methods in demonstrating the non-comparability of communities; i.e. is it easy or difficult to check the intersection of the diversity profiles of the communities when they are non-comparable. This is a practical point during the data analysis because there is no reason to use methods which poorly reflect the studied phenomena if we have better methods which are equally good in other respects.

Small, medium and large data sets were used to test the methods. The results of a small artificial data set, introduced in the Introduction, and a large semi-natural data set are presented in this paper. The large data set includes three communities with 31, 141 and 85 species, respectively. Both data sets were especially designed for this test: in the case of the small data set, communities A and B are non-comparable, i.e. the diversity profiles intersect, while C is more diverse than both A

and B. In the case of large data sets the first community is less diverse than the second and third ones, and the second and third communities are non-comparable.

Many other artificial and real data sets were used to evaluate the performance of the methods, but the examples presented here satisfactorily represent my experience in using these methods.

General model

Generally, a community A may be identified with the ordered pair $A = (S_A, n_A)$, where S_A is the number of species present and

$$n_A = \left(n_1, n_2, \ldots, n_i, \ldots, n_{S_A}\right)$$

is the abundance vector of the community and n_i is the abundance of the i-th species of the community. For our purposes it is often sufficient to know the relative abundances of species; thus a community may be identified by a pair (S_A, p_A), where p_A is the relative abundance vector of the species. When speaking generally about communities we frequently write simply (S, p) or just $p = (p_1, p_2, \ldots, p_S)$.

Using more formal terminology we can say that $(p_1, p_2, \ldots, p_S)$ is a discrete probability distribution and

$$\Gamma := \left\{(p_1, p_2, \ldots, p_S) : p_i \geq 0, \sum_{i=1}^{S} p_i = 1\right\}$$

is the set of discrete probability distributions containing S real numbers. The diversity is a real function defined on Γ, i.e.

$$D : \Gamma \to \mathbb{R}$$

where $\mathbb{R}$ is the set of real numbers. Patil & Taillie (1979) emphasized that community diversity can be defined as the average species rarity. Of course many different rarity functions, and thus many different diversity functions, can be defined. Denote the rarity of species i of the studied community (S, p) by $R(i; p)$; i.e. a numerical measure of rarity is to be associated with each species. Thus the diversity measure of a community (S, p) is defined as its average rarity:

$$D : \Gamma \to \mathbb{R}, \ D(p) : \sum_{i=1}^{S} p_i R(i; p),$$

In the following section the published one-parameter diversity index families will be reviewed, as well as other methods which can be used for diversity ordering.

Most of these were devised by mathematicians and subsequently adopted by ecologists. Two methods are new for the ecological literature.

Methods for diversity ordering

Rényi (1961) extended the concept of Shannon's entropy by defining the entropy of order α ($\alpha \geq 0$, $\alpha \neq 1$) of a probability distribution $(p_1, p_2, ..., p_S)$ as

$$H_\alpha = \left(\log \sum_{i=1}^{S} p_i^\alpha \right) \Big/ (1 - \alpha) \tag{1}$$

In this context, entropy is simply a synonym of diversity used in mathematics. It is the first published family of α-diversity indices. In the original definition the base number of the logarithm was 2; in ecological applications the natural logarithm is more frequently used.

Hill (1973) - who mentioned the work by Rényi (1961) - defined a diversity index family of order a ($a \geq 0$, $a \neq 1$) which is closely related to the previous one:

$$N_a = \left(\sum_{i=1}^{S} p_i^a \right)^{1/(1-a)} \tag{2}$$

I prefer to mention this family as the Exp(Rényi) diversity family. This family was introduced again by Patil & Taillie (1979, 1982), albeit from a different mathematical point of view. Their notation is S_β ($\beta \geq -1$; $\beta \neq 0$).

$$S_\beta = \left(\sum_{i=1}^{S} p_i^{\beta+1} \right)^{1/\beta} \tag{3}$$

The next family is that of entropy of type α, proposed by Daróczy (1970; Aczél & Daróczy 1975). Let $\alpha \geq 0$; $\alpha \neq 1$. Then the equation is:

$$H^\alpha = \left(\sum_{i=1}^{S} p_i^\alpha - 1 \right) \Big/ \left(2^{1-\alpha} - 1 \right) \tag{4}$$

It can be proven that Shannon's entropy is a limiting function of H^α when $\alpha \Rightarrow 1$, as in the case of Rényi's entropy, H_α. This family of entropies (diversities) can also be used for diversity ordering. This parametric family has not been used earlier in the ecological literature for diversity ordering.

Patil & Taillie (1979) proposed one more one-parameter diversity index family ($\beta \geq -1$; $\beta \neq 0$):

$$\Delta_\beta = \left(1 - \sum_{i=1}^{S} p_i^{\beta+1} \right) \Big/ \beta \tag{5}$$

They called it the diversity index of degree β (Patil & Taillie 1982).

The Right-tail-sum diversity is defined as follows (Patil & Taillie 1979):

$$T_i(p) = p_{(i+1)} + ... + p_{(s)} = \sum_{j=i+1}^{S} p_{(j)}, 1 \leq i \leq S$$

where $p_{(1)}, ..., p_{(S)}$ are the relative abundances of the species of a community arranged in descending order. If we consider i as a variable, then

$$\{ T_i(p) : i = 1, 2, ..., S \} \tag{6}$$

defines a one-parameter family of indices, while the diversity profile is defined by the polygonal path joining the successive points T_1, T_2, ..., T_S.

The Lorenz curve can also be used as a diversity profile (Taillie 1979). It can be displayed graphically by plotting and connecting the points

$$P_0 = (0,0), P_i = \left(\sum_{j=1}^{i} p_{(j)}, i/S \right). \tag{7}$$

Solomon (1979) proposed a diversity ordering based on the notion of majorization. He defined a partial order on Γ which is recommended for ordering communities according to their diversity. Let $p, q \in \Gamma$; the expression 'p majorizes q' means that

$$\sum_{j=1}^{i} p_{(j)} \geq \sum_{j=1}^{i} q_{(j)} \tag{8}$$

for each $i = 1, 2, ..., S-1$.

A k-dominance curve visualizes the dominance pattern of communities (Shaw et al. 1983). In a k-dominance plot percentage cumulative relative abundance (of the first k species) is plotted against log species rank (Lambshead et al. 1983, Platt et al. 1984); the percentage abundance of each species is ranked in decreasing order of dominance. In eq. 9 'i' is used instead of 'k' in order to be consistent with the other formulas, but the original name is k-dominance plot, which should be maintained:

$$\left(\log i, 100 \cdot \sum_{j=1}^{i} p_{(j)} \right) \tag{9}$$

This curve could be used for diversity ordering, but the lowest curve will represent the most diverse community; in this respect this method is just the opposite of the others and formally it is not a diversity ordering because the curve of a less diverse community is above the curve of a more diverse one over the whole range of the curve.

A method proposed here is related to both Right-tail-sum diversity and the k-dominance plot and can be called Logarithmic dominance ordering; it is defined by

$$P_i = \left(\log i, \sum_{j=i+1}^{S} p_{(j)} \right) \tag{10}$$

It can be displayed graphically by plotting and connecting the points P_i.

The next diversity index family is due to Hurlbert (1971):

$$S(m) = \sum_{i=1}^{S} \left\{ 1 - (1 - p_i)^m \right\} \tag{11}$$

It gives the number of species present when m individuals are drawn at random from the population. Conceptually m is an integer, but real values make mathematical sense. $S(m)$ is sometimes mentioned 'expected species diversity'. An important property of it is that an unbiased estimator for $S(m)$ is known. The minimum variance unbiased estimator for $S(m)$ as devised by Smith & Grassle (1977) is:

$$\hat{S}(m) = \sum_{i=1}^{S} \left\{ 1 - \binom{N - n_i}{m} \middle/ \binom{N}{m} \right\} \tag{12}$$

where

$$\binom{N}{m} = \frac{N!}{(N - m)! \, m!}$$

Eq. 12 is often called the Hurlbert-Smith-Grassle's diversity index family.

Executable programs of the diversity orderings discussed in the paper for IBM-compatible PCs (Tóthmérész 1993) are available from the author upon request (enclosing a formatted disk).

Relations of diversity orderings

The 12 methods of diversity ordering presented here will now be compared. First, two diversity index families are basically identical, the Rényi's and Hill's index

families. They differ only in their parametrization (see eqs. 1 and 2); their relation can be indicated as follows:

$$H_\alpha = \log(N_a), \quad N_a = \exp(H_\alpha)$$

Hill (1973) demonstrated that the three commonly used measures of diversity, Simpson's dominance index, Shannon's entropy, and the total number of species, are related to Rényi's definition of a generalized entropy for values of $a = 2$, 1 and 0, respectively.

The relation between N_a and S_β is evident from a comparison of eq. 2 with 3; by replacing β with $a - 1$, eq. 3 becomes identical with 2.

The relation between the entropy of order α and the entropy of type α (Daróczy 1970) follows from a comparison between eqs. 1 and 4 :

$$H_\alpha = \log_2 \left[\left(2^{(1-\alpha)} - 1 \right) H^\alpha \right] \middle/ (1 - \alpha)$$

and

$$H^\alpha = \left[2^{(1-\alpha)H_\alpha} - 1 \right] \middle/ \left(2^{1-\alpha} - 1 \right)$$

The relations between the Right-tail-sum diversity ordering, the Lorenz curve, Solomon's majorization, the dominance curve, and the Logarithmic dominance ordering are evident from eqs. 6 - 10; they are close relatives. The Lorenz curve is a graphical display of Solomon's majorization. The relation of the Right-tail-
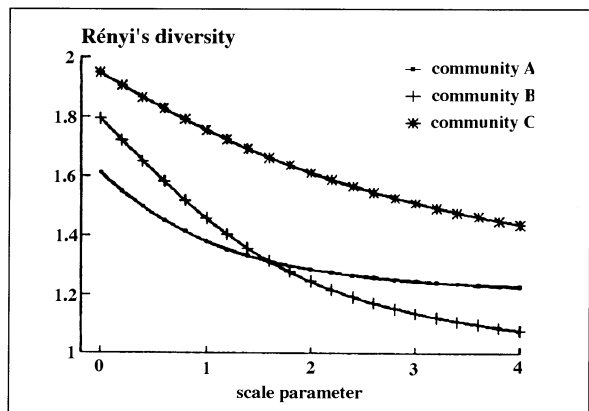

Fig. 1. Diversity ordering of three artificial communities using Rényi's index family. Community C is the most diverse (C > A and C > B). A and B are non-comparable because the diversity profiles are intersecting.
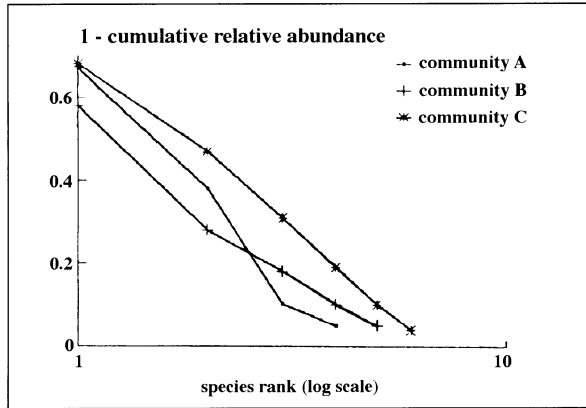
Fig. 2. Diversity ordering of three artificial communities using the Logarithmic dominance plot.
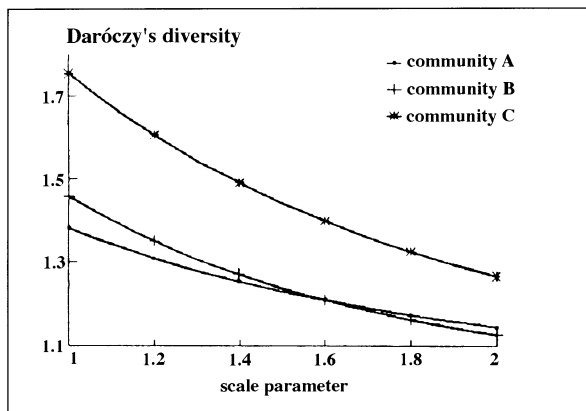

Fig. 3. Diversity ordering of three artificial communities using Daróczy's ordering. The graph is concentrated on the [1, 2] interval, which improves the presentation of intersection of the diversity profile of A and B.
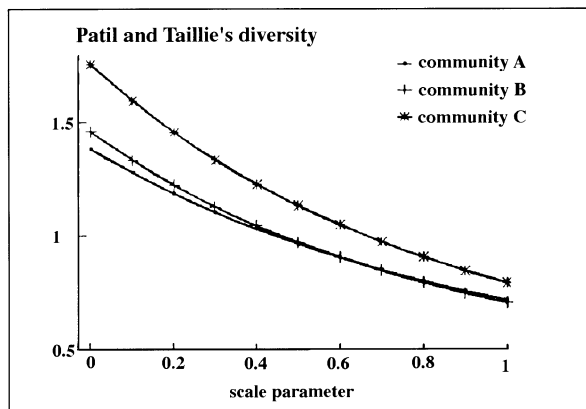

Fig. 4. Diversity ordering of three artificial communities using Patil & Taillie's ordering. The graph is concentrated on the [0, 1] interval, which improves the presentation of intersection of the diversity profile of A and B.

sum diversity and Lorenz curve or Solomon's majorization is straightforward as well:

$$T_i(p) = \sum_{j=i+1}^{S} p_{(j)} = 1 - \sum_{j=1}^{i} p_{(j)}$$

In the case of the Lorenz curve, however, the X and Y axes are interchanged relative to the right-tail-sum plot.

The Logarithmic dominance ordering is equivalent to the k-dominance plot after subtracting the k-dominance values from 100 and then dividing by 100:

log. dominance plot = (100 − k-dominance plot)/100.

It is also evident that the logarithmic dominance plot and the inverted k-dominance plot are identical after a multiplication by 100. Other relations between eqs. 6 - 10 can be demonstrated by simple calculations.

On the other hand, the diversity Δ_β of Patil & Taillie and the diversity index family of Hurlbert-Smith-Grassle are not related directly to the others.

Graphical comparison of diversity orderings

This comparison includes eight of the methods, covering the variation in approach, with emphasis on the usefulness, and with a special interest in the ability of the methods to demonstrate the non-comparability of communities; i.e. by displaying the intersection of diversity profiles.

For the small artificial data set, the Rényi, Exp(Rényi), Right-tail sum and Logarithmic dominance methods produced clear, easily interpretable results (Figs. 1 and 2). The figure produced by the Exp(Rényi) ordering is very similar to that produced by the Rényi ordering; the situation is the same for the Logarithmic dominance plot and Right-tail sum ordering; therefore these figures are not presented. Community C is clearly separated from the others and it is easy to realize the intersection of the diversity profiles of communities A and B. The figures produced by the Daróczy and Patil & Taillie methods are less clear (Figs. 3 and 4). Community C is well-separated from A and B, but it is difficult to detect the intersection of the diversity profiles of A and B (Figs. 2 and 3).

For the large data set, the Rényi and Logarithmic dominance orderings perform well (Figs. 5 and 6). The first community is well-separated from the others; it is evidently the least diverse. The intersection of the diversity profile of communities 2 and 3 is also well indicated by both methods. The Exp(Rényi) and Right tail sum orderings do not perform as well as these for the species-rich communities; the Right-tail sum ordering is par-
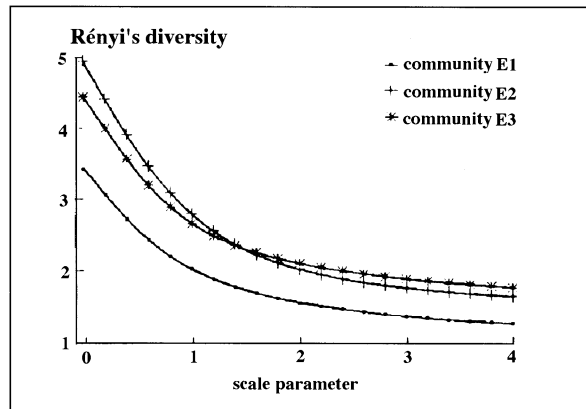
Fig. 5. Diversity ordering of three communities of the large data set using Rényi's index family. Community 1 is the less diverse; communities 2 and 3 are non-comparable because the diversity profiles intersect.
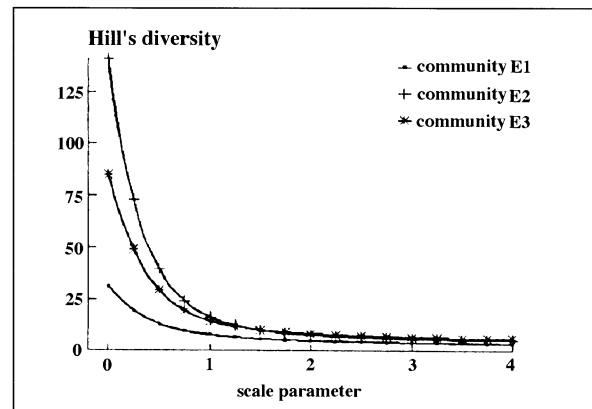

Fig. 7. Diversity ordering of three communities of the large data set using the Exp(Rényi) or Hill's diversity ordering. Evidently, community 1 is the least diverse, while the intersection of the diversity profiles of communities 2 and 3 is not displayed clearly.
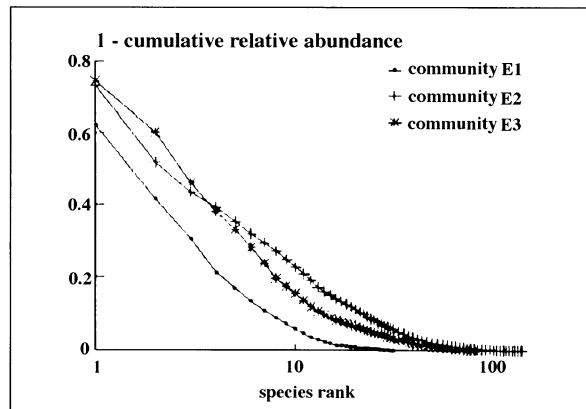

Fig. 6. Diversity ordering of three communities from the large data set using the Logarithmic dominance plot.
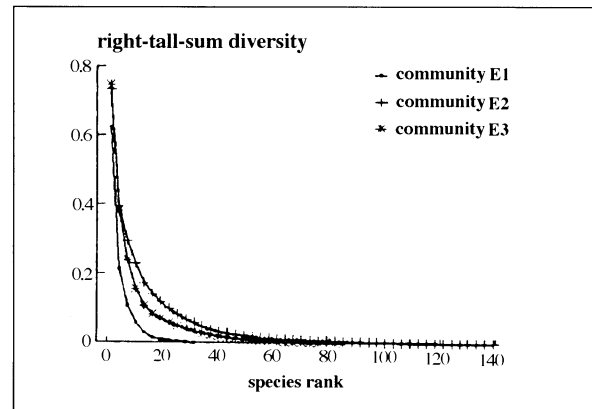

Fig. 8. Diversity ordering of three communities from the large data set using the Right-tail sum diversity ordering. The diversity orderings of the communities are poorly displayed. It is even difficult to detect that community 1 is the least diverse. The intersection of the diversity profiles of communities 2 and 3 are not displayed at all.

ticularly poor. Even the first community is hardly or not separated from the others and it is practically impossible to detect the intersection of the diversity profiles of the second and third communities (Figs. 7 and 8). The figures produced by the Daróczy and Patil & Taillie diversity orderings are very much the same; for species-rich communities they perform poorly.

The curve produced by the Hurlbert-Smith-Grassle diversity family indicates the relation of sample size and the number of species quite well but it is not especially effective in reflecting the intersection of diversity profiles (Fig. 9).

Discussion

Peet (1975) discussed the need for a theory of index response to facilitate the choice of diversity indices: one may wish the index to be sensitive to the composition of the dominant species but relatively indifferent to that of the rare ones. Changing the scale parameter of a diversity index family 'naturally' changes the sensitivity of the index family and plotting the diversities against the scale parameter, the change of the sensitivity can be displayed graphically. Therefore, while comparing communities by diversity profiles it is possible to trace
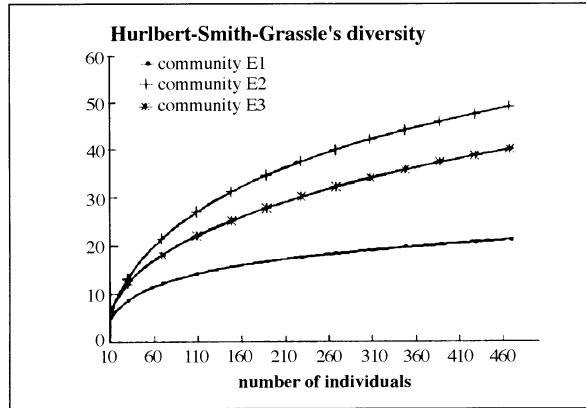
Fig. 9. Diversity ordering of three communities of the large data set using Hurlbert-Smith-Grassle's diversity ordering. The relation between sample size and species number of the communities is shown clearly, but it is rather difficult to figure out the diversity ordering of communities on the basis of this figure.

where the diversity ordering changes with respect to the dominant, subdominant or rare species. The diversity profiles may reveal ecological processes which lead to different patterns of dominance behaviour of species. That may be considered a very useful feature of the diversity profiles.

One of the most useful methods for ordering communities as to their diversity is Rényi's index family; it performs well irrespective of the species number of the community; the intersection of the diversity profiles is also well-indicated by this method. The Logarithmic dominance ordering also produced clear, well-interpretable figures for communities of different species richness levels. The Exp(Rényi) index family also presented good results, especially when the number of species is low. When the species number of the communities compared is medium or high it is better to use Rényi's index family or Logarithmic dominance plot ordering, while in the case of a medium or low species number the Exp(Rényi) index family may be useful as well. For species-poor communities the Right-tail sum ordering produced good figures.

When the differences between the species numbers of communities are medium or high, i.e. when one of the communities compared is much richer in species than the other(s), then the Rényi's index family or the Logarithmic dominance plot ordering may be practical as well. This result is also plausible from a theoretical point of view, because using a logarithmic scale on the Y-axis makes the Exp(Rényi) index family identical to

the Rényi one; the same holds for the Right-tail sum ordering and the Logarithmic dominance plot method.

This logarithmic transformation of the Y-scale is very effective in improving the visual quality of the figure when large differences occur in the species number of the compared communities.

Daróczy's entropies of type α and Patil & Taillie's diversity of index Δ_β are about equally effective, but Daróczy's method performed slightly better. The performance of these index families was better for small communities than for large communities.

Diversity ordering based on the Right-tail sum diversity was not effective in the case of large or medium species numbers, while it produced clear results in the case of small species numbers.

Calculation of the Hurlbert-Smith-Grassle's diversity index is extremely time-consuming as compared to the others. The curve produced is informative, but the method is not very effective in reflecting the intersection of the diversity profiles. It is almost impossible to detect the intersection of the diversity profiles by graphical inspection when one of the compared communities has a much larger number of individuals (shoots, etc.) than the others. The large difference in species number might produce similar effects but in a much lesser degree. The joint presence of these two factors might cause difficulties in the interpretation of the result of diversity ordering on the basis of purely graphical inspection.

References

Aczél, J. & Daróczy, Z. 1975. *On Measures of Information and their Characterizations.* Academic Press, New York, NY.

Cairns, J., Jr., Patil, G.P. & Waters, W.E. (eds.) 1979. *Environmental Biomonitoring, Assessment, Prediction and Management - Certain Case Studies and Related Quantitative Issues.* International Co-operative Publishing House, Fairland, MD.

Daróczy, Z. 1970. Generalized information functions. *Inform. Contr.* 16: 36-51.

Dennis, B., Patil, G.P., Rossi, O., Stehman, S. & Taillie, C. 1979. A bibliography of literature on ecological diversity and related methodology. In: Grassle, J.F., Patil, G.P., Smith, W. & Taillie, C. (eds.) *Ecological Diversity in*

Theory and Practice, pp. 319-353. International Cooperative Publishing House, Fairland, MD.

Goodman, D. 1975. The theory of diversity-stability relationships in ecology. *Quart. Rev. Biol.* 50: 237-266.

Grassle, J.F., Patil, G.P., Smith, W. & Taillie, C. (eds.) 1979. *Ecological Diversity in Theory and Practice.* International Co-operative Publishing House, Fairland, MD.

Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427-432.

Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52: 577-586.

Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113: 81-101.

Lambshead, P.J.D., Platt, H.M. & Shaw, K.M. 1983. Detection of differences among assemblages of benthic species based on an assessment of dominance and diversity. *J. Nat. Hist.* 17: 859-874.

Magurran, A.E. 1988. *Ecological Diversity and Its Measurement.* Croom Helm Ltd., London.

May, R.M. 1975. Patterns of species abundance and diversity. In: Cody, M.L. & Diamond, J.M. (eds.) *Ecology and Evolution of Communities*, pp. 81-120. Harvard University Press, Cambridge, MA.

Patil, G.P. & Taillie, C. 1977. Diversity as a concept and its implications for random communities. *Bull. Int. Stat. Inst.* 47: 497-515.

Patil, G.P. & Taillie, C. 1979. An overview of diversity. In: Grassle, J.F., Patil, G.P., Smith, W. & Taillie, C. (eds.) *Ecological Diversity in Theory and Practice*, pp. 3-27. International Cooperative Publishing House, Fairland, MD.

Patil, G.P. & Taillie, C. 1982. Diversity as a concept and its measurement. *J. Am. Stat. Ass.* 77: 548-567.

Peet, R.K. 1974. The measurement of species diversity. *Annu. Rev. Ecol. Syst.* 5: 285-307.

Pielou, E.C. 1975. *Ecological Diversity.* John Wiley and Sons, New York, NY.

Platt, H.M., Shaw, K.M. & Lambshead, P.J.D. 1984. Nematode species abundance patterns and their use in the detection of environmental perturbations. *Hydrobiologia* 118: 59-66.

Rényi, A. 1961. On measures of entropy and information. In: Neyman, J. (ed.) *Proceedings of the 4th Berkeley Symposium on Mathematical Statistics and Probability.* Vol. I., pp. 547-561. University of California Press, Berkeley, CA.

Resh, V.H. 1979. Biomonitoring, species diversity indices, and taxonomy. In: Grassle, J.F., Patil, G.P., Smith, W. & Taillie, C. (eds.) *Ecological Diversity in Theory and Practice*, pp. 241-253. International Cooperative Publishing House, Fairland, MD.

Shaw, K.M., Lambshead, P.J.D. & Platt, H.M. 1983. Detection of pollution-induced disturbance in marine benthic assemblages with special reference to nematodes. *Mar. Ecol. Progr. Ser.* 11: 195-202.

Smith, W. & Grassle, F.J. 1977. Sampling properties of a family of diversity measures. *Biometrics* 33: 283-292.

Solomon, D.L. 1979. A comparative approach to species diversity. In: Grassle, J.F., Patil, G.P., Smith, W. & Taillie, C. (eds.) *Ecological Diversity in Theory and Practice*, pp.

29-35. International Cooperative Publishing House, Fairland, MD.

Taillie, C. 1979. Species equitability: A comparative approach. In: Grassle, J.F., Patil, G.P. Smith, W. & Taillie, C. (eds.) *Ecological Diversity in Theory and Practice*, pp. 51-62. International Cooperative Publishing House, Fairland, MD.

Tóthmérész B. 1993. NuCoSA 1.00. Number Cruncher for Community Studies and other Applications. *Abstr. Bot.* 17: 283-287.

Washington, H.G. 1984. Diversity, biotic and similarity indices. A review with special reference to aquatic ecosystems. *Water Res.* 18: 653-694.