DIVORD 1.50: A PROGRAM FOR DIVERSITY ORDERING

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Abstract. The methods of diversity ordering, based on diversity profiles, have been developed as an improvement on diversity comparisons based on numerical valued diversity indices. A community A is said to be more diverse than that of B when the curve of the diversity profile of A is above of B on the whole range of a scale parameter. A program, DivOrd, is presented to calculate and display the diversity profiles of communities. Eight methods are included in the package. Mathematical background of the methods is also discussed. New results about the diversity index families are presented concerning their relations and characteristic features. Their usefulness is also assessed and a guideline is presented how to use and interpret the results during ecological studies. Density dependent and density independent representations are proposed and the effect of spatial pattern is also stressed. Their relations towards the direct spatial series analysis are also mentioned.

The program is written in Turbo Pascal and it is executable on any IBM-compatible PC having 640 Kbyte memory or more and VGA, EGA or Hercules graphics card. The program is completely menu-controlled.

Keywords one-parameter diversity index families, diversity profile, diversity ordering, density dependent and density independent representations, direct spatial series analysis

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Why should we use diversity profiles for diversity comparisons?

Different diversity indices may rank inconsistently a given pair of communities (Hurlbet, 1971). For example, two communities with the following abundances

A = (33, 29, 28, 5, 5), 5 species community

B = (42, 30, 10, 8, 5, 5), 6 species community

are ranked differently by the Shannon, H, and Simpson, D, indices:

$H(A) = 1.3808 < 1.4574 = H(B)$,

$D(A) = 0.7309 > 0.7194 = D(B)$.

Values of Shannon diversity was calculated by $H=-\Sigma p_i log p_i$ using natural logarithm. Simpson diversity was calculated by $D=1-[\Sigma n_i(n_i-1)]/[N(N-1)]$. n_i is the abundance and p_i is the relative abundance of the i-th species; $N=\Sigma n_i$.There are many reasons for this mis-ordering. Patil and 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 only a scalar quantity. A more straightforward illumination of the problem, provided by them, is related to the different sensitivities of diversity indices. The Shannon index is more sensitive to the effect of rare species; while the Simpson index tend to stress the effect of dominant species. A possible solution is to use parametric families of diversity indices instead of a numerical-valued diversity index. An important property of the family of diversity indices is their variable sensitivity to rare and abundant species. This means that communities can be compared for different "dominance levels" as a scale parameter changes. When we use a one-parameter family $\{D_\alpha: \alpha \text{ real}\}$ of diversity indices then the family may be portrayed graphically by plotting diversities D_α against the scale parameter α. This curve, the graph of $\{D_\alpha: \alpha \text{ real}\}$, is frequently mentioned as the diversity profile of the community (Patil and Taillie, 1979, 1982). In fact, α serves as a scale parameter; members of the D_α family have varying sensitivities to the rare and abundant species as α changes. Diversity profiles of communities A, B and

C = (32, 21, 16, 12, 9, 6, 4)

are presented in Fig. 1.

Using diversity profiles we can define the diversity ordering of communities in the following way: Community A is more diverse than community B (written A>B) when the diversity profile of A is above or equal to the diversity profile of B on the whole range of the scale parameter.

It can be shown that 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, B, either A>B or B>A; i.e. curves of two diversity profiles may intersect. In this case the two communities are not comparable; this means that we can find at least two diversity indices which order the communities differently. This situation might reflect important ecological processes which can be interpreted clearly; see for example Matus and Tóthmérész (1992), Tóthmérész et al. (1993). In Fig. 1 we can see that A and B are non-comparable, but that C>A and C>B.

While calculating diversities is very popular in theoretical and field ecology, diversity ordering based on parametric families of diversity indices is not frequently used. These methods involve more calculations than a simple diversity index. On the other hand they are relatively simple and more straightforward than the multivariate statistical methods. However, none of these are included in standard computer packages. NuCoSA might be an exception (Tóthmérész, 1991, 1993c). This software gap has delayed the spread of these methods.

Overview of diversity orderings

Historical notes

There are a long history and tradition of diversity in ecology. Tremendous lot of indices were published to measure it. These statistics were also used in other sciences, especially in physics. Statisticians also looked into the details of the characterization of "diversity". Rényi (1961) has published the first generalized entropy function. Generalized entropies are heavily used in physics nowadays (Hentschel and Procaccia, 1983). Based on this paper Hill (1973) derived a family of diversity indices and examined the usefulness of this unified notation. This index family is a straightforward derivation of the Rényi's entropy. Daróczy (1970) published another generalized entropy which also includes the Shannon diversity as a special case. At that time, ecologists did not recognize one of the most useful properties of these index families; i.e. they can be used for diversity ordering. It was recognized and emphasized by Patil and Taillie (1979); see also Solomon (1979). They had a very important contribution to the idea of diversity. They also proposed other families of diversity ordering.

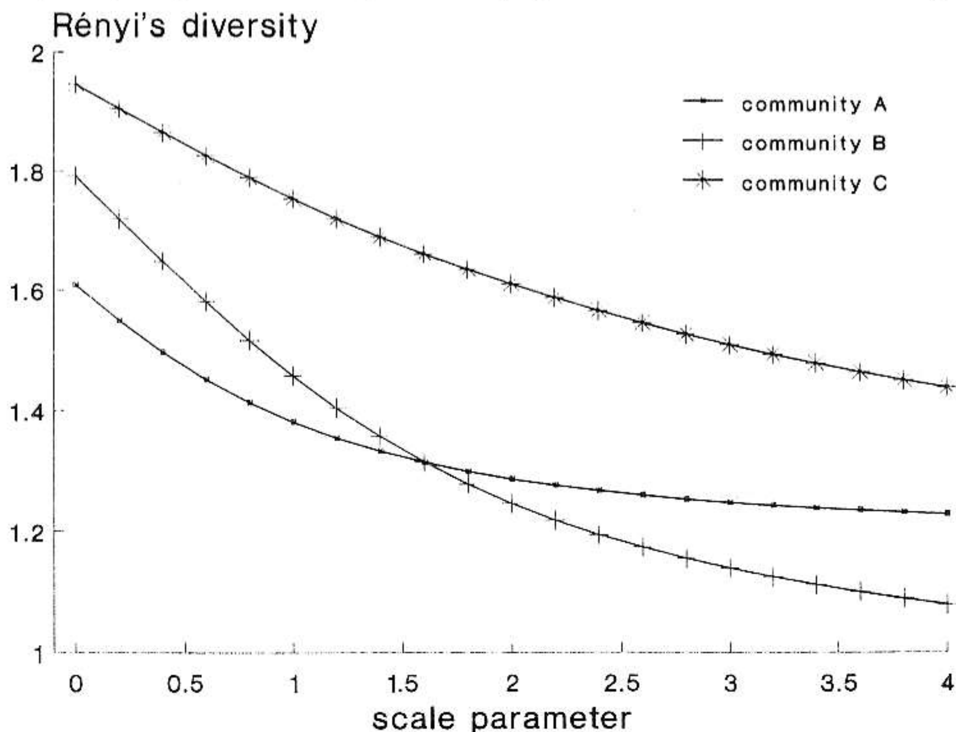


Fig. 1. Diversity ordering of three artificial communities using Rényi's index family. Community C is the most diverse (C>A and C>B). Communities A and B are non-comparable because the diversity profiles intersect.

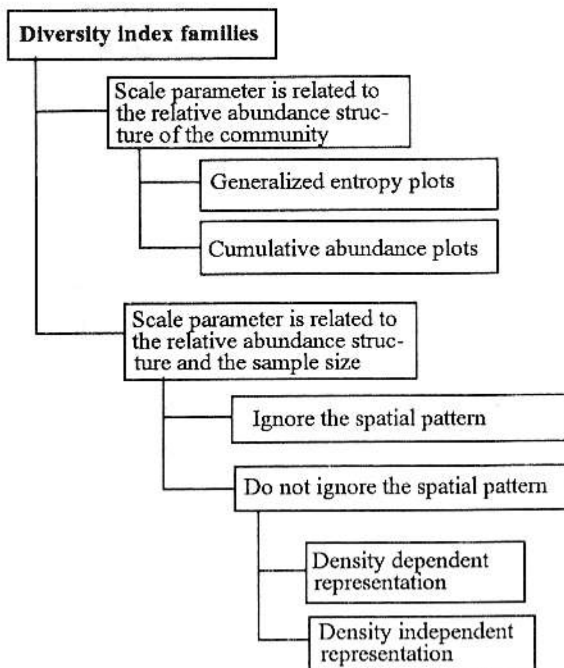


Fig. 2. Tree diagram of one-parameter diversity index families (diversity orderings).

Tóthmérész (1993b) reviewed the families which may be useful for diversity ordering; he also proposed a new one.

The story of rarefaction diversity, which also can be used for diversity ordering, is even more interesting. This is usually attributed to Saunders (1968) and/or Hurlbert (1971). A minimum variance unbiased estimation of it was published by Smith and Grassle (1977). However, this is nothing else just a species-individual curve which was invented in botany during the 1920's (Arrhenius, 1921; Gleason, 1922). That time there was a lot of discussion about the role of species-area and species-individual curves (Ashby and Stevens, 1935; Blackman, 1935). They even published many of the numerical formulas re-invented later in the same or a somewhat different context.

Types of diversity orderings

There are two main groups of diversity index families (Fig. 2). In the first group the scale parameter is related to the dominance structure of the community. In the second group there is a straightforward interpretation of the scale parameter related to different sample sizes. Thus, the meaning of the scale parameter is somewhat different for the two groups.

There are two subgroups of the first group; they can be mentioned as *generalized entropy plots* (GenE plots) and *cumulative relative abundance plots* (CuRe plots). All the diversity index families included in a subgroup are closely related; see the proofs in Tóthmérész (1993b). The first one includes the methods of Rényi, Hill, Daróczy, and Patil & Taillie; the second one contains the logarithmic dominance plot and right-tail-sum diversity plots. For the members of the first subgroup there is a scale parameter which is usually larger than 0 or -1; see Table 1. For the members of the other subgroup the range of the scale parameter is "automatically" the number of species.

Table 1. One-parameter diversity index families useful for diversity ordering. The name of the families is in the first column. The graph of an index family is displayed in the second column in the form of (x-coordinate, y-coordinate) which curve is the diversity profile. The third column contains the range of the family where the result is relevant from mathematical and ecological point of view.

Name	Graph	Range
Generalized Entropy Plots (GenE Plots)		
Rényi	$(\alpha, H(\alpha))$	$\alpha\geq 0, \alpha\neq 1$
Hill	$(\alpha, exp H(\alpha))$	$\alpha\geq 0, \alpha\neq 1$
Daróczy	$(\alpha, DH(\alpha))$	$\alpha\geq 0, \alpha\neq 1$
Patil & Taille	$(\beta, D(\beta))$	$\beta\geq -1, \beta\neq 0$
Cumulative Relative Abundance Plots (CuRe Plots)		
Logarithmic dominance plot	$(log i, T(i))$	$i=1,...,S$
Right tail sum plot	$(i, T(i))$	$i=1,...,S$
Rarefaction Diversity Plots		
Logarithmic species-individual plot	$(log m, S(m))$	$m>0$
Logarithmic species-area plot	$(log A, S(A))$	$A>0$

There is a sophisticated relationship between the diversity orderings of the second group and the direct spatial series analysis. It is evident that the diversity of a community also depends on the spatial structure. Strongly aggregated or segregated appearance of the species may heavily decrease the diversity. It is not possible to represent the effect of pattern in diversity comparisons except for the members of the second group. In the traditional form these methods also ignore the spatial structure of the community. Indeed, when the spatial structure is included we should speak about direct spatial series analysis. The spatial series analysis, however, needs special sampling techniques (Juhász-Nagy, 1976; Juhász-Nagy and Podani, 1983; Tóthmérész and Erdei, 1992); thus, these are not included in the package. This needs a special package like MULTI-PATTERN (Erdei and Tóthmérész, 1993).

It can be proved that all these families are equivalent from the point of view of ordering (Patil and Taillie, 1979). It does not involve, however,

that there is no reason to use the others. Tóthmérész (1993b) demonstrated studying the graphical properties of the diversity orderings that different methods may be useful for different data sets depending on the community structure, sample size, number of species, etc. Another important feature of the species-area and species-individual relations the possibility of the density dependent and density independent representations and the close relationship to the direct spatial processes (Tóthmérész, 1993a).

Diversity orderings implemented in the program

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

$n_A=(n_1,n_2,...,n_i,...,n_{S(A)})$

is the abundance vector of the community and n_i is the abundance of the i-th species of the community. Frequently enough 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.

Patil and Taillie (1979) stressed the view that community diversity can be defined to be the average species rarity. Many different rarity functions, and thus many different diversity functions can be defined. The one-parameter diversity index families implemented in the program are displayed in Table 1. The diversity index families are defined in the following way.

Entropy of order α (Rényi, 1961):

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

Entropy of type α (Daróczy, 1970; Aczél and Daróczy, 1975)

$$DH(\alpha)=\left(\sum_{i=1}^{S} p_i^{\alpha}-1\right)/(2^{1-\alpha}-1)$$

Diversity index of degree ß (Patil and Taillie, 1979):

$$D(\beta)=\left(1-\sum_{i=1}^{S} p_i^{\beta+1}\right)/\beta$$

Right-tail-sum diversity (Patil and Taillie, 1979; Solomon, 1979):

$$T(i)=p_{(i+1)}+...+p_{(S)}=\sum_{j=i+1}^{S} p_{(j)}$$

where $p_{(1)},...,p_{(S)}$ are the relative abundances of the species of a community arranged in descending order.

Rarefaction diversity (Saunders, 1968; Hurlbert, 1971) or species-individual curve:

$$S(m)=S-\sum_{i=1}^{S}(1-p_i)^m$$

The expected number of individuals in an area is proportional to the size of the area. Therefore, we can calculate the species-area curve (Blackman 1935) using the following relationship
where N is the total number of individuals on the area.

Smith and Grassle (1977) presented the minimum variance unbiased estimation of S(m) as:

$$\hat{S}(m)=S-\sum_{i=1}^{S}\binom{N-n_i}{m}/\binom{N}{m}$$

where

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

An important property of family of indices is its variable sensitivity to rare and abundant species. A precise definition of sensitivity is given by Patil and Taillie (1982). For large values of the scale parameter, GenE plots are sensitive to abundant species, whereas they are sensitive to rare species for smaller values of the scale parameter.

Table 2. The relation of the magnitude of scale parameter and the sensitivity of diversity orderings.

	Value of the scale parameter	
Name	small	large
GenE plots	sensitive to effect of rare species	sensitive to the effect of dominant species
CuRe plots	sensitive to effect of dominant species	sensitive to the effect of rare species
Rarefaction plots	sensitive to effect of dominant species	sensitive to the effect of rare species

The pattern of sensitivity of the CuRe plots are opposite to that of GenE plots: they are sensitive to abundant species for small "i" and to rare species for large "i". In the case of rarefaction curves the

pattern of sensitivity is the same as with CuRe plots.

Special cases and interpretation of index families

It is important to know some special cases of diversity index families to interpret the result of diversity orderings.

For the Rényi's diversity ordering the following relations are valid.

$H(-\infty)$ = logarithm of the reciprocal of the relative abundance of the rarest species. This is mentioned just because of the completeness of the special values because it was proposed not to use scale parameter values less than 0.

$H(0)$ = logarithm of the total number of species;

$H(\alpha\to 1)$ = Shannon index;

$H(2)$ = logarithm of the reciprocal of Simpson's index;

$H(+\infty)$= logarithm of the reciprocal of the relative abundance of the commonest species. This is the logarithm of the reciprocal of Berger-Parker index (Berger and Parker, 1970).

The following special cases can be mentioned for the Patil and Taillies's diversity index family.

$D(-1)$= total number of species - 1

$D(\beta\to 0)$ = Shannon index

$D(1)$ = Simpson index

Finally for the species-individual relationship the following cases may be mentioned.

$S(2)$ = (1 + Simpson index);

$S(+\infty)$ = total number of species.

When m is a positive integer, $S(m)$ is the expected number of species to be found in a hypothetical random sample of size m. For a given community, the plot of this index versus m is the expected species-individual curve. There is mathematical sense of $S(m)$ for a noninteger m value. In direct spatial series analysis there is ecological sense as well (Tóthmérész, 1993a).

$D(\beta)$ of Patil and Taillie can be interpreted as the number of species that a completely even community would need to have its diversity to be the same as that of the studied community. Thus, sometimes it is mentioned as *equivalent number of species*. *exp*$H(\alpha)$ also can be interpreted this way.

How to use the program

Place the DivOrd diskette into the A: disk drive. Copy the DIVORD.EXE file to your hard disk. From the root directory, type COPY A:\DIVORD.EXE then press <ENTER>. Preferable you should copy the program into a subdirectory instead of the root directory.

To activate the program, type DIVORD and press <RETURN>. Then one page of information appears, and if you press any key you can see the main menu (Fig. 3).

```
1 - Data Input

Generalized Entropy Plots (GenE Plots)
  2 - Rényi
  3 - Hill
  4 - Daróczy
  5 - Patil & Taillie

Cumulative Relative Abundance Plots (CuRe Plots)
  6 - Logarithmic Dominance Plot
  7 - Right-Tail-Sum Diversity Plot

Rarefaction Diversity Plots
  8 - Species-Individual Curve (Density Independent)
  9 - Species-Area Curve (Density Dependent)

10 - Other Samples to Compare
11 - Result to Disk in HG Format

12 - Exit

Your choice :
```

Fig. 3. The main menu of the DivOrd program.

The program takes data from data files and not directly from the keyboard. The instructions for the arrangement of data input files are in the "Arrangement of input data" Chapter. This version of the program can handle data matrices containing 50 samples and 200 species (50 rows and 200 columns). The "Data Input" option is used to load data matrices into the program in the following way. First the name of the file is requested (Fig. 4).

```
Name of Input File = DEMO.DAT
```

```
There are 3 sample units.

How many curves do you want to draw (less than or equal to 4) ? 2

Please type the identity number of the sample sites:
  1.: 1
  2.: 3
```

Fig. 4. Data Input screens of the DivOrd program. In the "DEMO.DAT" file there are 3 samples and the diversity profile of the 1st and 3rd samples (communities) are asked to draw.

Then, the computer informs you about the

number of communities (sampling units) contained in the data matrix and then the number of communities (sampling units) to be compared is asked (Fig. 4).

The computer informs you when the data file cannot be found, for example, owe to mistyping of the file name. Then you have to use again the "Data Input" option to load data into the program. After finishing the data input procedure successfully you are in the main menu again and you can select a diversity ordering.

Range of the scale parameters during the previous run :

Start = 0.000

End = 4.000

Step = 0.250

New run with other range <y/RETURN> ?

Fig.5. The menu of changing the range of scale parameter and the steps of calculations.

In the case of the GenE plots the pre-defined range of the scale parameter is the [0,4] interval for Rényi's and Hill's ordering, [0,2] for Daróczy's, and [-1,2] for Patil & Taillie's. If you press any key the diversity profiles disappear and you can choose another range of the scale parameter (Fig. 5). You can also change the step-size of the calculations; using larger steps the calculation is faster but the curve might not be as smooth as using an optimal step size. There is no reason to use a scale parameter higher than 10. Very frequently 4 or 6 is excellent as an upper bound; sometimes 3 is enough. For practical reasons the program is designed not to use parameter values higher than 15 or 20.

Finally, the "Other Samples to Compare" option allows you to choose other communities (sampling units) to be compared from the same data set. First the program informs you again about the number of communities (sampling units) in the data matrix as in the case of choosing the "Data Input" menu and then you proceed in exactly the same way as before.

The figures presented by the DivOrd program can be included into papers directly using the GRAB.EXE utility of WordPerfect or any other utility distributed with high quality word processors. There is a special option in the DivOrd to save the results into as ASCII file in a special format which can be used directly to import into the HarvardGraphics program package. Thus, you can produce high quality figures comfortably. You should consult the documentation how to use HarvardGraphics. We present a short description how to import ASCII data into the HarvardGraphics.

1. Select "Create new chart" at the main menu and then "bar/line chart". There you must select "number" as X data type. Finally press F10; see Fig. 6.

2. At the Main Menu, select Import/Export.

3. At the "Import/Export" menu, select Import ASCII data.

The Select File screen appears. (a) Select an

```
                         Bar/Line Chart Data

   Title:
Subtitle:
Footnote:

                         X Data Type Menu

  Pt      Name        Day         Week      Month     Quarter   Year
          Month/Day   Month/Yr    Qtr/Yr    Time      Number

          X data type:   Number

          Starting with:                 Ending with:
          Increment:

F1-Help          F3-Save          F5-Set X type                   F9-More series
F2-Draw chart    F4-Draw/Annot    F6-Calculate     F8-Options     F10-Continue
```

Fig. 6. "Bar/line chart" menu of the HarvardGrafics.

```
                          Import ASCII Data
 1 Rényi's diversity
 2
 3
 4    0.0000   1.6094   1.7918   1.9459
 5    0.2000   1.5500   1.7202   1.9044
 6    0.4000   1.4973   1.6494   1.8643
 7    0.6000             Import Titles and Legends
 8    0.8000
 9    1.0000
10    1.2000    Import title and subtitle:              ►Yes    No
11    1.4000    Import first line as series legends:   Yes   ►No
12    1.6000
13    1.8000
        1        2        3        4

  Read data by          ►Line   Column      Read from line    4    to line    243
  Tabular data format  ►Yes    No          Read from column  1    to column  4

F1-Help        F3-Select files
               F4-Reselect                        F8-Options          F10-Continue
```

Fig. 7. "Import ASCII dat" menu of the HarvardGraphics.

ASCII file to import. Then the Import ASCII Data screen appears; Fig. 7. (b) If you have already imported from an ASCII file, the Import ASCII Data screen appears. Press F3 to display the Select File screen and then go to step 4.

4. Set the options on the Import ASCII Data screen as displayed by Fig. 7.

5. Press F10.

You are the "Bar/Line Chart Data" menu and you can use the options to define the final form of the figure.

Arrangement of the input data

The program reads ASCII files in the form of a two-way table; i.e. an n by m data matrix is used, where n (rows) is the number of communities (sampling units) to be studied and m (columns) is the total number of species in the samples or any other characteristics measured for each sample. The data matrix must be full; i.e. missing values are not admissible. The first line of the data file must consist of a label for the data set which will help you to identify the data. The maximum length of the label is 159 characters. The second line contains two figures separated by spaces. The first figure is the number of rows in the data matrix. The second figure is the number of columns of the data matrix. It does not matter how many spaces are between the two figures; the line might also begin with space characters.

On the third line the data matrix starts, in free format. The items of the matrix must be separated by a space or spaces; the number of spaces and the arrangement of the matrix is entirely free. It is practical, however, to arrange the figures as a table because this can be useful for other purposes and easy to check and correct.

It is easy to create these data files using any spreadsheet program package such as Quattro, Excel, Symphony or Lotus 1,2,3 or by using the full-screen editor of the DOS5 or any word processor and saving the data in DOS text file format. The file named "DEMO.DAT", distributed with the DivOrd program is presented in Fig. 8.

```
Diversity ordering (noncomparable communities); DEMO.DAT
 3  7
33 29 28  5  5  0  0
42 30 10  8  5  5  0
32 21 16 12  9  6  4
```

Fig. 8. The "DEMO.DAT" data file distributed by the DivOrd program.

The data matrix in Fig. 9 contains 3 samples of 7 species. In the first sample there are 33 individuals from the first species; there are 29 individuals from the 2nd species, 28 from the 3rd species, etc. Similarly, we can say that the 1st species is represented by 33 species in the first community (sample) and by 42 individuals in the 2nd one and it is represented by 32 individuals in the 3rd community (sample). Thus, the data matrix is organized as it is shown in Fig. 9.

	species 1	species 2	species 3
sample 1	33	29	5
sample 2	42	30	10
sample 3	32	21	16

Fig. 9. The arrangement of data items in the data file used by the DivOrd program.

Guideline to the applications of the methods

Graphical comparison of diversity orderings

Tóthmérész (1993b) compared the diversity orderings according to their effectiveness in displaying the differences of community structures. He was stressing a practical point of view: which methods were the most useful during the graphical inspection of data comparing the diversity of communities.

One of the best method for ordering communities was Rényi's index family irrespectively of the species number of the communities; the intersection of the diversity profiles was well-indicated by this method. Logarithmic dominance ordering also produced clear, well-interpretable figure for communities of all size. For species-poor and moderately species-rich communities Hill's index family was useful; for species-poor communities the right tail sum ordering also performed well.

When the differences between the species number of communities are medium or high (i.e. when one of the compared communities are much richer in species than the others) then also the Rényi's index family or logarithmic dominance plot was useful.

Calculation of rarefaction diversities was overly time-consuming compared with the others in the case of unbiased minimum variance estimation. The curves produced by rarefaction diversities clearly indicated the relation of sample size and the number of species but it was not especially effective in reflecting the intersection of diversity profiles. The logarithmic scaling of the x-axis, however, highly improved the figure. Plotting them this way they were also very useful for both small and large communities.

Density dependent and density independent representations

Evidently the number of species in a sample depends on the number of individuals which can be found in the sample. The density of vegetation, however, is frequently different for the compared communities. We are interested in the diversity pattern of the communities and the density has a "scaling" effect. Therefore, depending on the goal of the study, it may be useful a density independent representation of the rarefaction diversity profiles. Density dependent and density independent representations evidently may produce different diversity ordering relations as it is demonstrated by Fig. 10. Here B>A, but the density of community B was higher. Using a density independent or density-free representation of the rarefaction diversity profiles, we can see that the communities are non-comparable. The possibility of density dependent and density independent representations are extremely useful in ecological research; see an application in Tóthmérész and Matus (1993). There is no such possibility for GenE and CurE plots.

Complementarity of GenE and CuRe plots

GenE plots depend strongly on the number of species because at the starting point of the diversity profile they take the value of the number of species or a value directly related to it, like S-1 or *log*S. CuRe plots are heavily depend on the abundance of the most abundant species. From this point of view these methods are exactly complementary. Lets compare the diversity of the communities of the first Chapter to a community

A' = (29, 29, 28, 5, 5)

which is almost identical with A; the abundance of the first species is 29 instead of 33. Using one of the GenE plots evidently A<B but it is rather difficult to recognize that A'<>B. The diversity profiles intersect for a scale parameter value which is larger than 16 and it is almost impossible to recognize the intersection. On the other hand the non-comparability is evident using one of the CuRe plots; see Fig. 11.

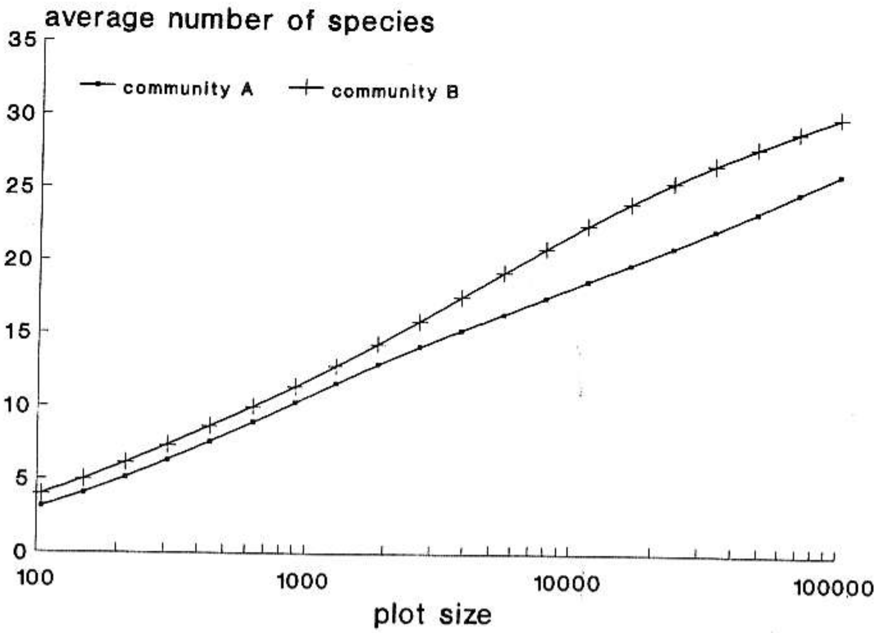
It is easy to produce an example which is the "opposite" of the above mentioned. Lets compare the following communities:

E1 = (790, 74, 19, 123, 50, 3, 25, 13, 28, 37),

E1' = (790, 74, 19, 123, 50, 3, 25, 13, 28, 37, 1, 1),

E2 = (8, 60, 55, 45, 8, 7, 14, 4, 1, 75, 45).

The first and the third communities are almost identical; the only difference is that in the community E1' two new species are included with 1-1 individuals. Using a CuRe plot it is rather difficult to detect that E1'<>E2, however, it is evident using a GenE plot; see Fig. 11.



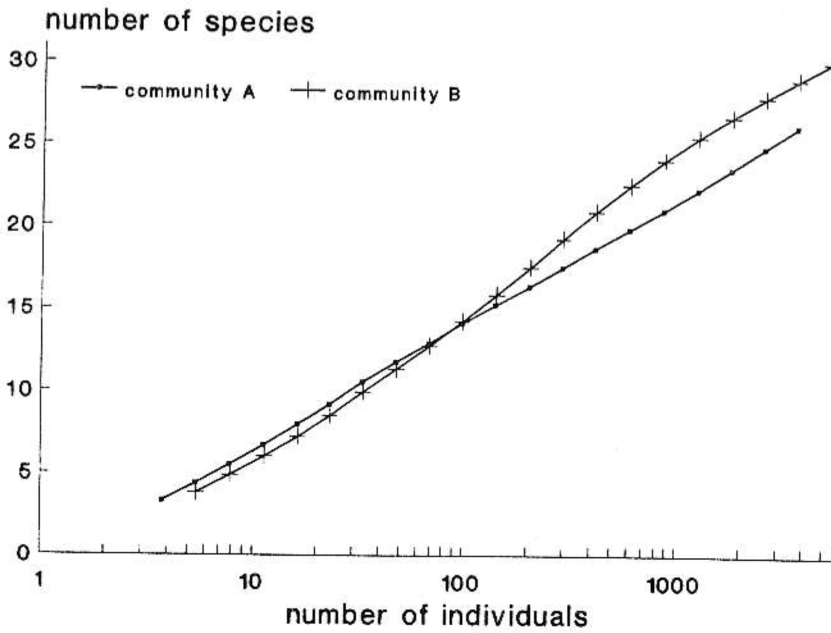


Fig. 10. Density dependent and density independent representation of the diversity profiles of the same communities.

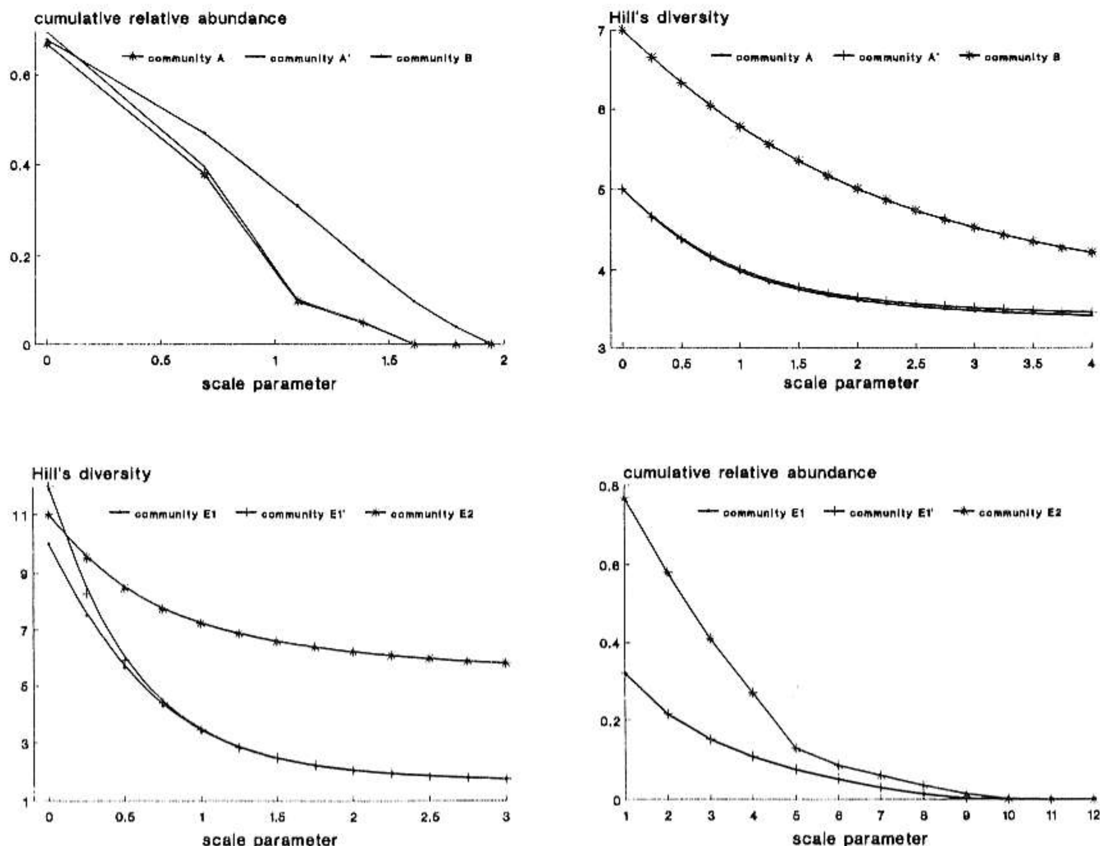


Fig. 11. Complementarity of the GenE and CuRe plots from the point of view of displaying the non-comparability of communities.

The effect of grazing

Matus and Tóthmérész (1992) and Tóthmérész and Matus (1993) studied the effect of moderate cattle grazing to the structure of a sandy grassland in Eastern Hungary. This region is characterized by inland dunes having been formed during the Pleistocene. The studied meadow is not sustained or stabilized by the grazing; the grazing is not part of the ecosystem here.

There were 33 species in the ungrazed case and 36 in the grazed one. 30 species were detected in both transects. The species-individual diversity of the ungrazed community was 2.2757 and 2.2269 for the grazed community using the corrected Shannon formula proposed by Hutcheson (1970), the difference is not high, yet it is significant in statistical sense using the analog of t-test developed for comparing diversities. Another interesting fact was that the grazed community was more species rich while the ungrazed community was more diverse. The diversity profiles of the communities intersected; for the rare species the cattle grazed community was more diverse while the ungrazed community was more diverse for the dominant and subdominant species. Therefore, the moderate grazing decreased the diversity of dominant species; the abundance of these species also decreased. At the same time the number of rare species and their diversity increased. The situation was much more sophisticated using rarefaction diversity ordering with special emphasis on the effect of the distributional pattern (Tóthmérész et al., 1993).

Diversity orderings and spatial processes

The rarefaction curves are well known in botany and zoology as species-area and species-individual curves; more exactly these are the species-area or species-individual curves of a "random" or unstructured community. However, the diversity of a community heavily depends on the pattern. The importance of the patchiness on the community level was recognized very early in botany; see

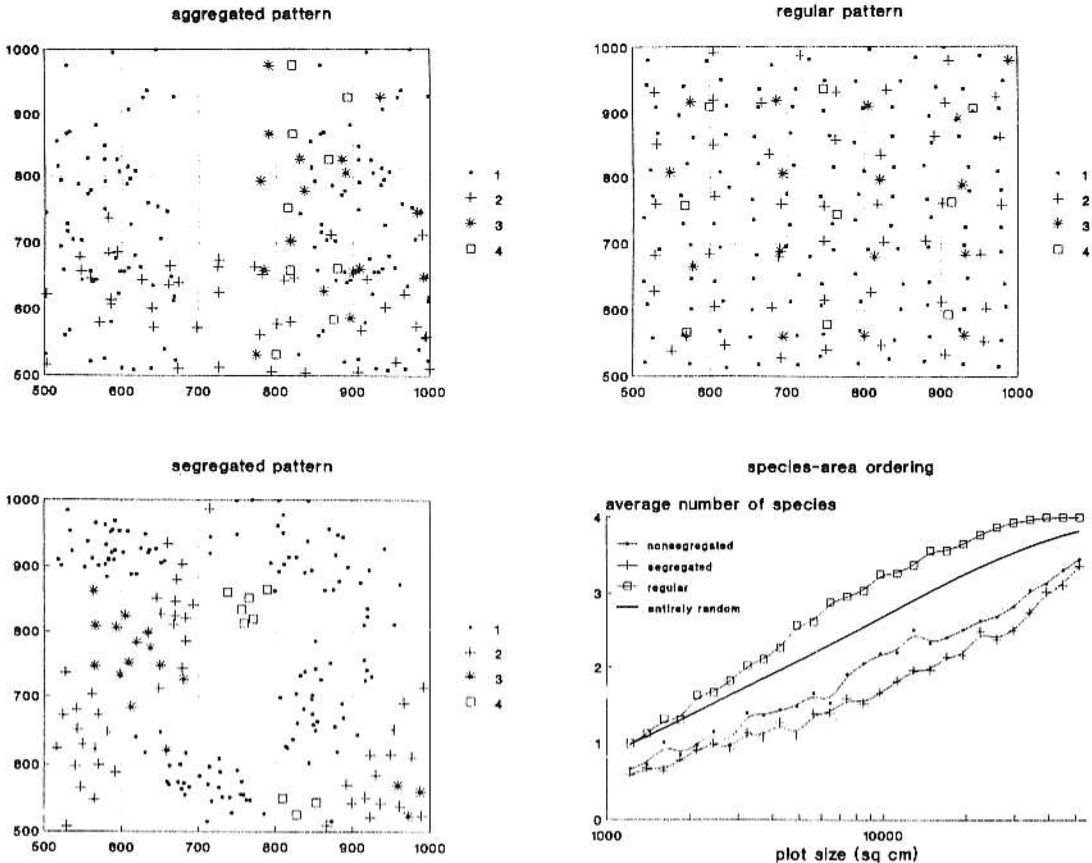


Fig. 12. The effect of spatial pattern on rarefaction diversity ordering.

Godwin and Conway (1939), Watt (1925, 1937). Watt (1947) suggested that plant communities are comprised of a mosaic pattern of patches which are dynamically related to each other. Ecologists always professed the importance of multispecies patterns; see Watt (1947). This is also confirmed by the fact that Watt's seminal paper is the most frequently cited paper in the ecological literature (McIntosh, 1989).

The effect of pattern to the species richness is demonstrated by the Fig. 12. Each community has exactly the same number of species and the same number of individuals; therefore the S(m) curve is the same for each community if we ignore the spatial pattern. The distribution of individuals, however, are strikingly different. The number of species was counted for 50 plots for each plot size and the average number of species was plotted against the plot size. The communities are well ordered; the community having regular pattern is the most diverse; the aggregated community is less diverse than the totally random, unstructured community. The less diverse is the segregated community where the distribution of individuals is aggregated and there is a strong segregation between the species; i.e. the patches usually contain one or only few species.

Table 3. The relation of rarefaction diversity orderings and direct spatial series analysis.

	density dependent	density independent
expected (random)	species-area curve	species-individual curve
observed (field)	direct spatial series analysis: location-type statistics for number of species in the plots	direct spatial series analysis: location-type statistics for the number of species in a sample of N individuals

That is a very significant feature of the rarefaction diversity orderings. All the other methods ignore the spatial pattern of the communities. To utilize this important feature of the rarefaction diversity ordering we need a special sampling tech-

nique which reflect the spatial arrangement of the individuals. The relation of rarefaction diversity orderings and direct spatial series analysis is demonstrated by Table 3. A more detailed discussion of direct spatial series analysis can be found in Tóthmérész (1993a).

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References

Aczél, J. and Daróczy, Z. (1975): On Measures of Information and their Characterizations. - Academic Press, New York, San Francisco, London.

Arrhenius, O. (1921): Species and area. - J. Ecol. *9*, 95-99.

Ashby, E. and Stevens, W.L. (1935): The quantitative analysis of vegetation. - Annals of Botany *49*, 779-802.

Berger, W.H. and Parker, F.L. (1970): Diversity of planktonic Foraminifera in deap sea sediments. - Science *168*, 1345-1347.

Blackman, G.E. (1935): A study by statistical methods of the distribution of species in grassland associations. - Annals of Botany *49*, 749-777.

Daróczy, Z. (1970): Generalized information functions. - Information and Control *16*, 36-51.

Erdei, Zs. and Tóthmérész, B. (1993): MULTI-PATTERN 1.00. A program package to analyze and simulate community-wide patterns. - Tiscia *27*, 45-48.

Gleason, H.A. (1922): On the relation between species and area. - Ecology *3*, 156-162.

Godwin, H. and Conway, V.M. (1939): The ecology of a raised bog near Tregaron, Cardiganshire. - J. Ecol. *27*, 313-359.

Hentschel, H.G.E. and Procaccia, I. (1983): The infinite number of generalized dimensions of fractals and strange attractors. - Physica *8D*, 435-444.

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.

Hutcheson, K. 1970: A test for comparing diversities based on the Shannon formula. - J. Theor. Biol. *29*, 151-154.

Juhász-Nagy, P. (1976): Spatial dependence of plant populations. Part 1. - Acta Bot. Hung. *22*, 61-78.

Juhász-Nagy, P. and Podani, J. (1983): Information theory methods for the study of spatial processes and succession. - Vegetatio *51*, 129-140.

Matus, G. and Tóthmérész, B. (1992): Detecting the effect of grazing on the community structure of a grassland by traditional methods and information statistics. - "The State of Art in Vegetation Science", International Association for Vegetation Science Symposium of the Working Group for Theoretical Vegetation Science, Toledo.

McIntosh, R.P. (1989): Citation classics in ecology. - Q. Rev. Biol. *64*, 31-49.

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

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

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

Saunders, H. L. (1968): Marine benthic diversity: a comparative study. - Am. Nat. *102*, 243-282.

Smith, W. and 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. and Taillie, C. (eds.): Ecological Diversity in Theory and Practice , International Coowrative Publishing House, Fairland, Maryland, pp. 29-35.

Tóthmérész B. (1991): NuCoSA 1.00. A program package: Number Cruncher for Community Studies and other Applications. - Conference of the International Association for Vegetation Science, Eger, Hungary.

Tóthmérész, B. (1992): Comparative analysis of different methods of diversity orderings: A case study. - "The State of Art in Vegetation Science", International Association for Vegetation Science Symposium of the Working Group for Theoretical Vegetation Science, Toledo.

Tóthmérész, B. (1993a): Statistical analysis of spatial pattern of communities. - Preprint of the Ecological Institute of Kossuth L. University, Debrecen, Hungary.

Tóthmérész, B. (1993b): Comparative analysis of different methods of diversity orderings. - Submitted to Journal of Vegetation Science.

Tóthmérész, B. (1993c): NuCoSA 1.00: Number cruncher for community studies and other applications. - Abstracta Botanica *18*.

Tóthmérész, B. and Erdei, Zs. (1992): The effect of species dominance on information theory characteristics of plant communities. - Abstracta Botanica *16*, 43-47.

Tóthmérész, B., Matus, G. and Molnár, A. (1993): Does intermediate disturbance really increase the number of species? - "Species coexistence and diversity maintenance in temperate grassland ecosystems". Conference organized by the Institute of Botany, Academy of Sciences of the Czech Republic, Bedrichov.

Watt, A.S. (1925): On the ecology of British beechwoods with special reference to their regeneration. Part II. The development and structure of beech communites of the Sussex Dows. - J. Ecol. *13*, 91-112.

Watt, A.S. (1937): Studies in the ecology of Breckland. II. On the origin and development of blow-outs. - J. Ecol. *25*, 91-112.

Watt, A.S. (1947): Pattern and process in the plant community. - J. Ecol. *35*, 1-22.