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DIVERSITY AND EVENNESS STATISTICS

ABSTRACT: The recent concepts of diversity and evenness and their definitions are discussed. It is shown that especially the ambiguities in defining evenness has led to confusion about evenness measures and their applicability. Definitions of diversity and evenness from parameters of relative abundance distributions avoid such ambiguities. In this paper diversity is defined as the negative inverse of the slope of the relative abundance distribution in a semilogarithmic plot and evenness as the arcus tangens transformed shaping parameter. Diversity and evenness depend therefore on the type of relative abundance distribution and diversities from communities of different types of relative abundance distributions (power fraction, random assortment or Zipf-Mandelbrot type) cannot be compared directly. The properties of these newly defined diversity and evenness indices and their behavior in samples are discussed. It is shown that Tokeshi's newly developed power fraction model may serve as a universal basis for defining diversity and evenness indices.

KEY WORDS Relative abundance distributions, diversity, evenness, power fraction, random assortment, Zipf-Mandelbrot Model

1. INTRODUCTION

The use of diversity and evenness measures has a long tradition in ecological research and is one of the major tools in studies of community structure and for comparisons

of communities. They also play a central role in conservation biology. Recently, the concept of diversity has become central in the renewed debate about the relation between diversity and community stability and ecosystem functioning (Tilman 1996, Naeem and Li 1997, Grime 1997, Grady-Steed *et al.* 1997, Hooper and Vitousek 1998, Sankaran and McNaughton 1999, Tilman 1999). However, despite the long use in research and despite many papers on the mathematics, the characteristics, and the deficiencies of certain indices (see reviews in Whittaker 1972, Peet 1974, Pielou 1977, Magurran 1988, Lande 1996, Smith and Wilson 1996) no consensus had been reached concerning the question what the various evenness and diversity indices really measure and how to define strictly what is meant by evenness (Kvælsteth 1991, Lande 1996, Smith and Wilson 1996, Hill 1997).

The most often used measures of diversity are Simpson's index of concentration

$$H_{VD} = \frac{1}{\sum_{i=1}^S p_i^2} \quad (1)$$

derived from the probability that two randomly chosen individuals of a community are from the same species and the Shannon information measure

$$H_H = - \sum_{i=1}^S p_i \ln(p_i) \tag{2}$$

where p_i is the relative abundance of the i -th species from a community of S species. It is frequently overlooked (May 1975, Pielou 1977) that both measures are very similar (except for very uneven and ecologically unrealistic communities). Their interrelation may be described by a regression derived from Fig. 1

$$H_H = \ln\left(\frac{H_{VD}}{2}\right) + 1 \tag{3}$$

The traditionally associated evenness measures are

$$E_H = \frac{H_H}{\ln(S)} \tag{4}$$

and

$$E_{VD} = \frac{H_{VD}}{S} \tag{5}$$

From equations 3, 4, and 5 we also get the interrelation between both evenness measures

$$E_H = \left(\frac{\ln(E_{VD}) - \ln(2) + 1}{\ln(S)} \right) + 1 \tag{6}$$

Another often used measure of diversity is the parameter α of the log-series relative abundance distribution, defined by

$$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right) \tag{7}$$

with N being the total number of individuals.

Due to the deficiencies of the above two evenness indices (they are not independent of species numbers and rely heavily on sample size) many alternative indices have been proposed (for instance Heip 1974, Molinari 1989, Nee *et al.* 1992, Camargo 1993, Bulla 1994, Hill 1973, 1997). In their review of evenness indices, Smith and Wilson (1996) advocated the use of the (for species numbers) calibrated slope of the relative abundance distribution in a log abundance – species rank order plot

$$E_Q = - \frac{2}{\Pi} \arctan(S \times b) \tag{8}$$

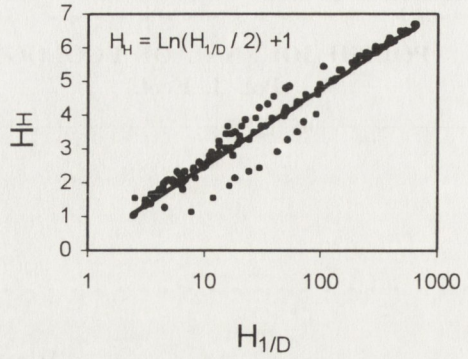


Fig. 1. A: Relationship between the diversity indices of Shannon (H_H) and Simpson ($H_{1/D}$) derived from 170 assemblages following power fraction models with parameter values k between -1 and 3 and species numbers between 5 and 1000 as described in the methods section. The points ranging far below and above the regression line all stem from assemblages of 10 or less species.

with b being the slope. The arcus tangens transformation serves to force the index into a $0-1$ scale.

Another index of evenness based on the variance of the log transformed relative densities, strongly recommended by Smith and Wilson (1996) and studied by Weiher and Keddy (1999) is

$$E_{var} = 1 - \frac{2}{\Pi} \arctan\left(\frac{\sum_{i=1}^S (\ln(p_i) - \frac{\sum_{i=1}^S \ln(p_i)}{S})^2}{S}\right) \tag{9}$$

Again, the arcus tangens transformation serves to force the index into a $0-1$ scale. It should be noted that this index is very similar to the Gaussian width (the standard deviation of the log transformed densities). In the case of a power fraction type model, for instance, it is nearly the inverse quadrate of it, random assortment type models result in a sigmoidal relation and Zipf-Mandelbrot models in hyperbolic ones (plots not shown). The Gaussian width is often used to describe relative abundance distributions (Sugihara 1980, Tokeshi 1993) but depends strongly on species numbers (especially at low species numbers) which makes the index not well suited for measuring evenness.

The question remains what do these indices really measure and what are the ecological foundations of them. The traditional view interprets diversity as the combined effect of species number and their relative abundances (Schaefer 1983) or (largely being the

same) as a measure of the joint effects of species number and evenness of a community (Pielou 1977). Such a definition between evenness E and diversity H can be expressed by a simple equation (Magurran 1988):

$$H = E \times f(S) \quad (10)$$

With $f(S)$ being a function that depends on the species number s . However, such an implicit definition does not tell what is in fact measured by both variables and a part of the confusion stems from this ambiguity. For instance the classical textbooks (Begon *et al.* 1986, Krebs 1995) and reviews (May 1975, Pielou 1977, Lande 1996) but also most modern practitioners treat H_H , $H_{1/D}$, and α as measures of diversity. Whittaker (1972) and Tokeshi (1993), however, noticed that H_H is rather a measure of evenness (of equitability in the words of Whittaker) but treated $H_{1/D}$, and α further as diversity (or dominance) measures. From equation 3 follows that for $H_{1/D}$ this is then impossible. The view that $H_{1/D}$ (and therefore H_H too) is indeed a measure of evenness was also expressed by Camargo (1993, 1995).

The parameter α of the log-series model was strongly recommended by Taylor *et al.* (1976), Taylor (1978), and Rosenzweig (1995) as a diversity measure although the latter author self admits that α is constant for all communities of the same relative abundance distribution. This is clear because α describes nothing more than the slope of the log series, the geometric or the random assortment model in a log abundance – species rank order plot (in the following shortly termed slope). But, in the case of the geometric model the slope has long been interpreted as a measure of evenness (Motomura 1932, Tokeshi 1993), a combination which is logically impossible.

Due to the confusion concerning the interpretation of the various diversity statistics the situation for evenness indices is not better. Camargo (1995) was surely right in stating that “at the present time there is great confusion on how to measure

and interrelate species evenness and associated parameters of community structure”.

In part, this confusion stems from the fact that there is no concern about how to define evenness. One school starts from the intuitive notion that the slope of the log (abundance) – species rank order plot tells something about evenness. If all species have the same abundance this slope is zero and a maximum evenness is reached (Fig. 2). Such a view has been followed by Bulla (1994), Camargo (1995), Smith and Wilson (1996), and Hill (1997). Another view (Whittaker 1972, May 1975, Routledge 1983) states that all communities of the same relative abundance distribution should have the same evenness. That means, for instance, that all communities following a canonical log-normal distribution or a power fraction model with identical shape parameter have the same evenness (Fig. 2). However, May himself gives in Table 1 of his classical paper (May 1975) for the canonical log normal ($E_H = 2\Pi^{-1/2} / \ln(S)^{-1/2}$) and for the broken stick ($E_H = 1 - 0.42 / \ln(S)$) equations for the evenness which are clearly not independent of species number and the relation between E_H and $E_{1/D}$ in equation 5 also depends on S .

Sometimes, both ways in defining evenness are mixed which further adds to the confusion about the matter. For instance, Smith and Wilson (1996) in their review of evenness indices took the slope to measure evenness but also treat the density sequence 1497, 1, 1, 1 (4 species) and multiples of it (for higher species numbers) as a test of independence of an index on species number. Such sequences all have the same community structure, but their slopes in log density species rank order plots are different.

Another point that serves attention is that communities following different relative abundance distributions may react different on diversity and evenness measures. Frequently, a log-series serves as a starting point for a definition on an index (Routledge 1983, Hill 1997). In this case the difference in definition between diversity and evenness index is hidden by the fact that in a log-series (or a random as-

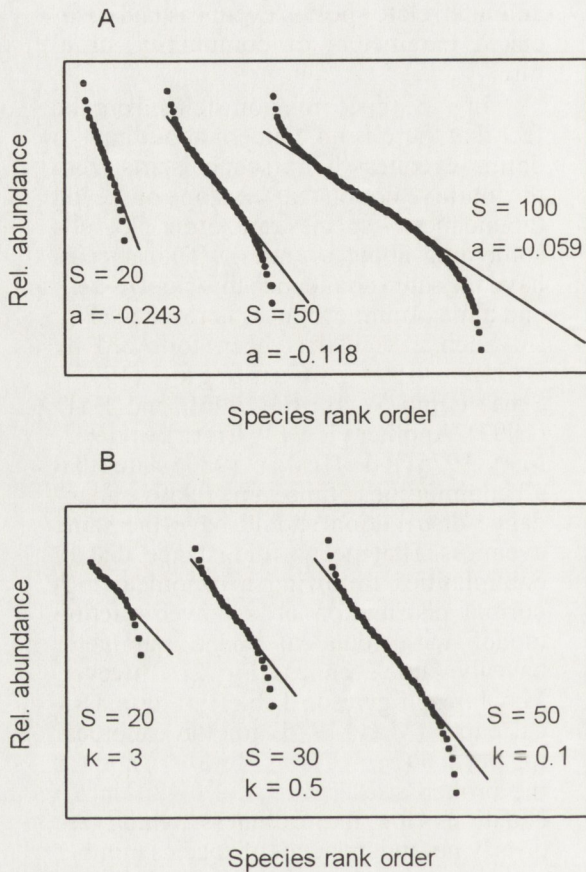


Fig. 2. Assemblages following power fraction models with different species numbers (S) and resulting slope values a . A: 3 assemblages with a shape generating parameter $k = 0.1$. B: 3 assemblages with the same slope $a = -0.12$.

sortment or a geometric series) slope of the log abundance – species rank order plot and shaping parameter are either identical or related by a constant factor but independent of species number. In other distributions, such as a log-normal, a Sugihara fraction or a Zipf-Mandelbrot model, shape parameters and slope are connected by the number of species according to equation 10 (see below). In this case the type of relative abundance distribution matters when defining diversity and evenness indices and will influence the way an index behaves.

The use of the shaping parameters of relative abundance distributions as measures of diversity and evenness has been advocated by various authors (Whittaker 1972, Kempton and Taylor 1976, Taylor 1978, Tokeshi 1993), however, in the case of log-normal or Zipf-Mandelbrot distributions the existence of two shaping parameters has prevented the use of them as diversity statistics. In this respect the development of the power fraction model by Tokeshi (1996) may mark a breakthrough (see part I for computation procedures, Ulrich 2001b). This

model is driven by a single shaping parameter and encloses the whole range of the traditional sequential breakage and log-normal models. The model therefore allows to separate the effects of shaping parameter and slope on diversity and evenness indices and may help to clarify both concepts.

In the following study the behavior of the above mentioned diversity and evenness statistics will be compared using three different stochastic relative abundance distributions representing the three main types of distributions which were identified in the first part of this study (Ulrich 2001b): the power fraction model, the random assortment and a stochastic version of the Zipf-Mandelbrot model. It will be shown how they are related to the model parameters.

2. MATERIALS AND METHODS

For the present study 170 assemblages (in this study assemblage always refers to model communities, whereas community is

used for real ones) each of a power fraction, a random assortment, and a stochastic version of the Zipf-Mandelbrot model (with only one shaping parameter) were generated giving a total of 510 assemblages. The models are described in detail in Tokeshi (1996) and in the first part of this study (Ulrich 2001b). Because they are stochastic models species densities of each of these assemblages were mean values of 100 replicates each. Table 1 shows the species number and parameter combinations of these assemblages. The parameters were chosen to span over the whole range of possible and biologically realistic shapes. Excluded from further analysis were a few of these assemblages where the least abundant species had relative densities below 10^{-15} .

H_H is for all three types of models a logarithmic function. For α this relation is a hyperbola. That means H_H and α are in fact estimates of the slope of the relative abundance distributions in semilogarithmic plots.

The evenness indices studied were neither strongly correlated with the slope of the distributions nor with the shaping parameter k . Only E_H and E_{var} showed a good correlation with k in the case of power fractions models (Figs 4 and 5). E_Q which measures the calibrated slope of the distribution and $E_{1/D}$ performed not better (data not shown). That means the existing evenness indices measure something not immediately connected with RADs. It means also that communities of the same type of distribution with the same shap-

Table 1. Species numbers (S) and parameter values (k) of 510 assemblages from three different relative abundance distributions generated for this study. See Tab. 1 of part I of this study (Ulrich 2001b) for generating algorithms

Model	S	k
Power fraction	5, 10, 15, 20, 25, 30, 50, 75, 100,	3, 2, 1, 0.5, 0.2, 0.1, 0, -0.1, -0.5, -1
Random assortment	150, 200, 300, 400, 500, 600, 800, 1000	0.03, 0.05, 0.075, 0.1, 0.15, 0.2, 0.25, 0.3, 0.5, 1
Stochastic Zipf-Mandelbrot		1, 1.25, 1.5, 1.75, 2, 2.5, 3, 4, 5, 6

For each assemblages H_H , $H_{1/D}$, E_H , $E_{1/D}$, α , E_{var} , E_Q as well as slope (a) and intercept (b) of the middle ranking 70% of species of the log (abundance) – species rank order plot were computed.

3. RESULTS

3.1. DEFINING DIVERSITY AND EVENNESS MEASURES

What do diversity measures measure? Fig. 3 shows for assemblages following power fraction, random assortment and Zipf-Mandelbrot distributions that the slope value of the log abundance – species rank order plots is highly correlated with H_H and α independent of species number. E_H – and the other evenness indices of which the data are not shown - are not correlated with slope. The regression between slope and

ing parameters have not necessarily the same evenness when this is measured by E_H , E_{var} , E_Q or another index. For instance, two communities following canonical log-normal distributions but with different species numbers may have different evenness values. This apparently contradicts the common view of evenness.

The above result implies that the indices may depend on species number. Fig. 6 shows that contrary to recent literature claims (Smith and Wilson 1996, Weiher and Keddy 1999) none of the tested evenness indices is independent of species number. Best performs E_H . For relative abundance distributions similar to a classical canonical log-normal (power fraction with $k = 0.1$) E_H is nearly independent of species number. The other indices mostly decrease at higher species numbers, a fact which has implications for published evenness studies (Weiher and Keddy 1999, Wilson *et al.* 1999, Ulrich 2001a).

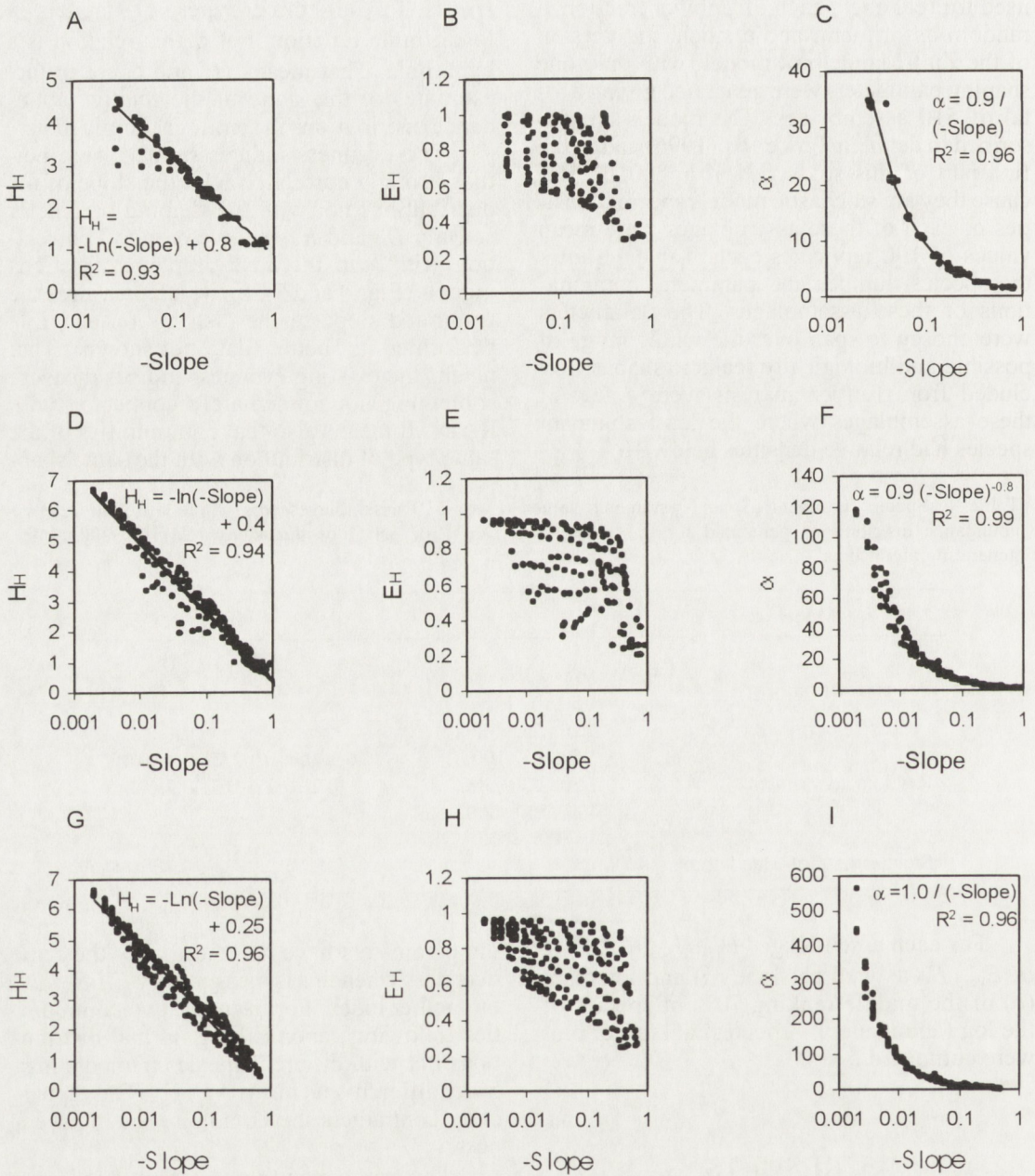


Fig. 3. Relationships between the slope of the log abundance - species rank order plot and H_H , E_H , and α (equations 2, 4, and 7 in the introduction) of 170 assemblages each following a random assortment (A, B, C), a power fraction (D, E, F), and a stochastic Zipf-Mandelbrot (G, H, I) RAD. Given are also the regression functions. R^2 - variance explanation of the regression. Notice the different scales for H_H and α .

The above results show that only diversity measures can unambiguously be connected with features of relative abundance distributions. They leave open the question of a strict definition of evenness.

If diversity measures slope than it seems convenient to define evenness in terms of the shaping parameter of a relative abundance

distribution. Such a concept implies that all distributions with the same set of parameters have the same evenness. Another attractive feature is that evenness then is by definition independent of species number. The definitions imply however that there can't be one measure for all distributions. Each shape of RAD has accompanying evenness and diver-

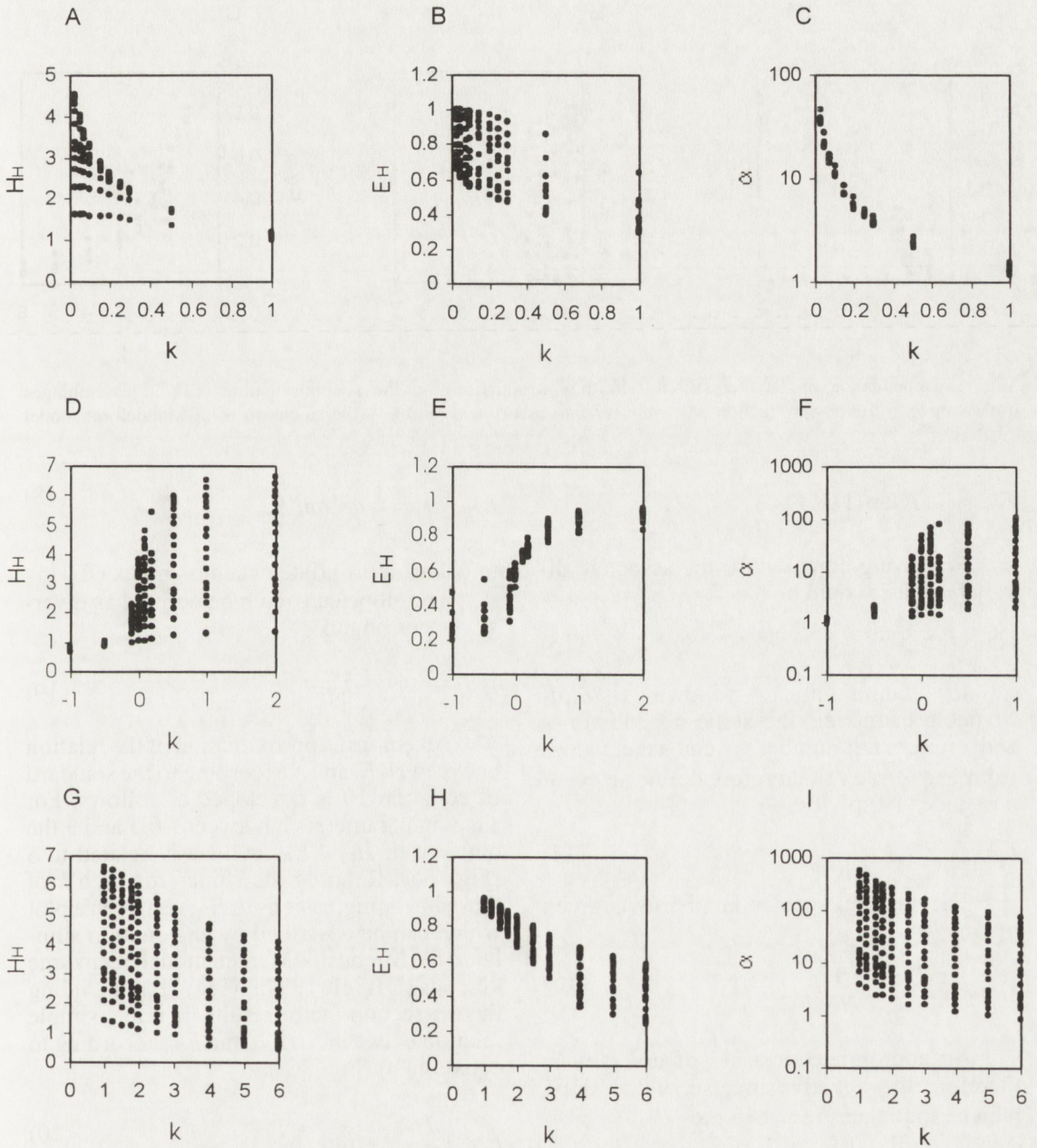


Fig. 4. Relationships between the shape parameter k and H_H , E_H , and α of 170 assemblages each following a random assortment (A, B, C), a power fraction (D, E, F), and a stochastic Zipf-Mandelbrot (G, H, I) RAD.

sity indices. They also imply that diversities from communities of different types of relative abundance distributions cannot be compared directly. This fact had been obscured by the existing indices.

The simplest form is met in the case of communities following random assortment, or geometric or log-series RADs. For a random assortment model

$$\text{Slope} = -k \ln(2) \quad (11)$$

The slope is therefore independent of species number. If we take k which ranges from 0 to $+\infty$ as a starting point of a measure of evenness it is convenient to use an arcus tangens transformation of the inverse of k then. This leads to a measure that is 0 at minimal and 1 at maximal evenness.

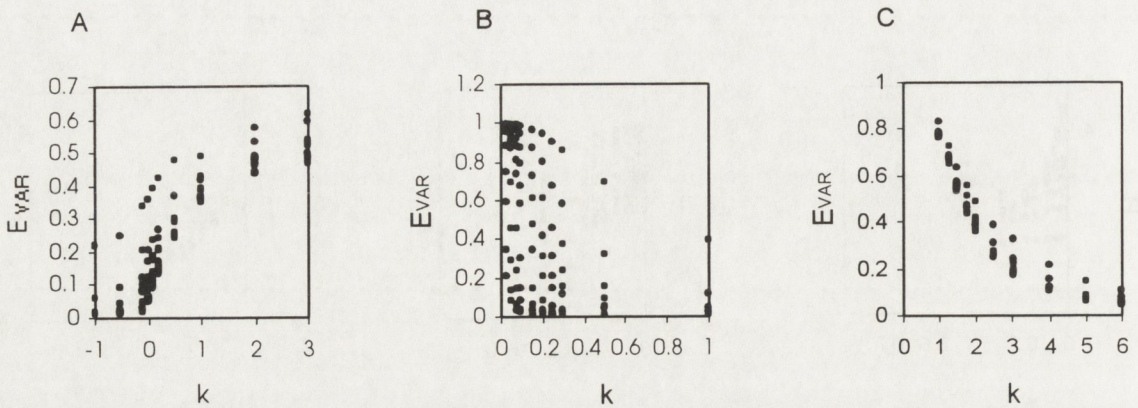


Fig. 5. Dependence of E_{var} (equation 9 in the introduction) on the shaping parameter k in assemblages following A – the power fraction, B – the random assortment, and C – the stochastic Zipf-Mandelbrot model of RAD.

$$E_{RA} = \frac{2}{\pi} \arctan(1/k) \tag{12}$$

Following equation 10 the associate diversity index would be

$$H_{RA} = E_{RA} S \tag{13}$$

In communities following Zipf-Mandelbrot models the slope depends on k and on species number. k can take values from 1 to ∞ . We can therefore define an evenness index simply by

$$E_{ZM} = 1/k \tag{14}$$

The slope at species number S is given by

$$Slope = \frac{d \ln(S^{-k})}{dS} = \frac{-k}{S} \tag{15}$$

An appropriate measure of diversity is therefore the negative inverse of the slope which range then from 1 to $+\infty$

$$H_{ZM} = S/k \tag{16}$$

Both definitions can be combined via the standard of equation 10:

$$H_{ZM} = S E_{ZM} \tag{17}$$

More difficult is the case in communities being described by a power fraction model (Sugihara fraction, log-normal, random fraction and others (see Tokeshi 1993). The shaping parameter k of the power fraction model may take values between $-\infty$ and $+\infty$. It is therefore again convenient to transform k into a 0–1 range by

$$E_{PF} = k' = \frac{1}{\pi} \arctan(k) + \frac{1}{2} \tag{18}$$

to get an appropriate evenness index (E_{PF}).

The slope can again be defined as diversity according to

$$H_{PF} = -1 / slope \tag{19}$$

An empiric approximation of the relation between H , E , and S according to the standard of equation 10 is developed as follows. For shaping parameters k between -0.3 and 3 the quotient of H_{PF} / E_{PF} is linearly related to S (Fig. 7A). Relating the slopes for each k of these linear regressions to E_{PF} results in a plot which can be described by an equation similar to the Michaelis-Menten model of enzyme kinetics (Ulrich 1999a) (Fig. 7B). Including this correction factor results then in a simple relation between S , H_{PF} , and E_{PF} according to equation 10 (Fig. 7C).

$$E_{PF} \approx \frac{H_{PF}}{S} + 0.4 \tag{20}$$

with a minimum value of 0.4. Equation 18 gives a minimum evenness of 0.4 for $k = -0.3$. For smaller shaping parameters equation 20 does not hold. However, the range of -0.3 to 3 encloses nearly all k -values up to now recorded (Sugihara 1980, Tokeshi 1996, Ulrich unpubl.).

Equations 13, 17, and 20 show that for each type of relative abundance distribution there is a simple relation between diversity and evenness. These relations equal the classical form defined by $H = Ef(S)$ (Magurran 1988).

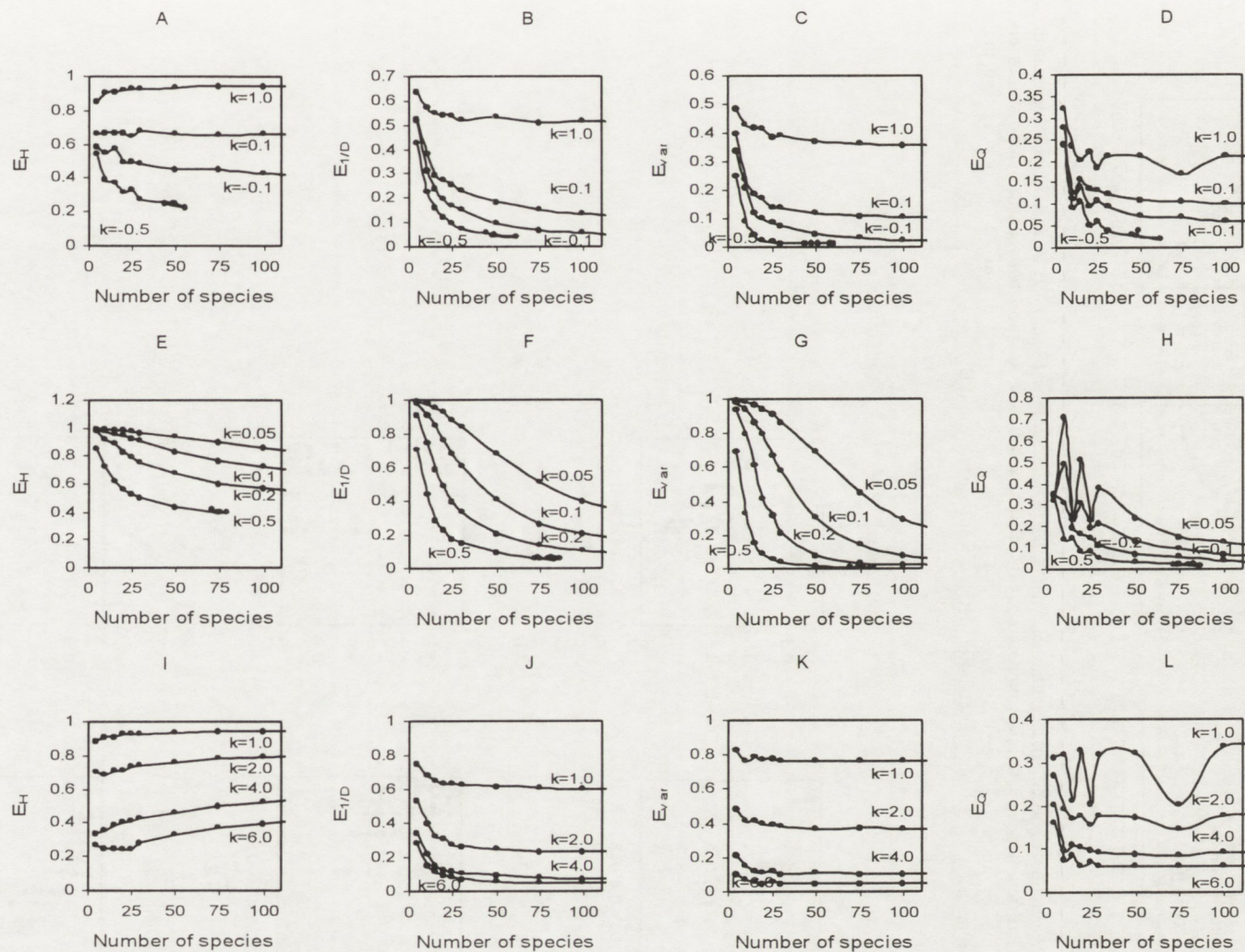


Fig. 6. Dependence of four measures of evenness (E_H , $E_{1/D}$, E_{var} , and E_Q ; equations 4, 5, 8, and 9 in the introduction, respectively) on the number of species of 170 assemblages each. A to D: Random assortment model, E to H: power fraction model, I to L: stochastic Zipf-Mandelbrot model. For each model the shape parameters k are given.

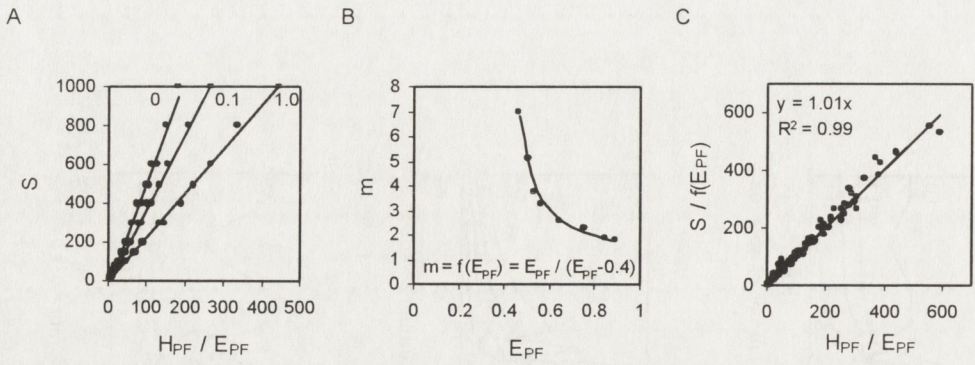


Fig. 7. A: Relation between species number S and H_{PF}/E_{PF} (equations 18 and 19) of assemblages generated with three different power fraction models ($k = 0$, $k = 0.1$, $k = 1.0$). B: Relation between the slope values $m (=f(E_{PF}))$ of the linear regressions of Fig. 7A and E_{PF} for 8 k -values from 3.0 to -0.1 . Given is also the resulting regression. C: Testing the equation derived from Figs 7 A and B.

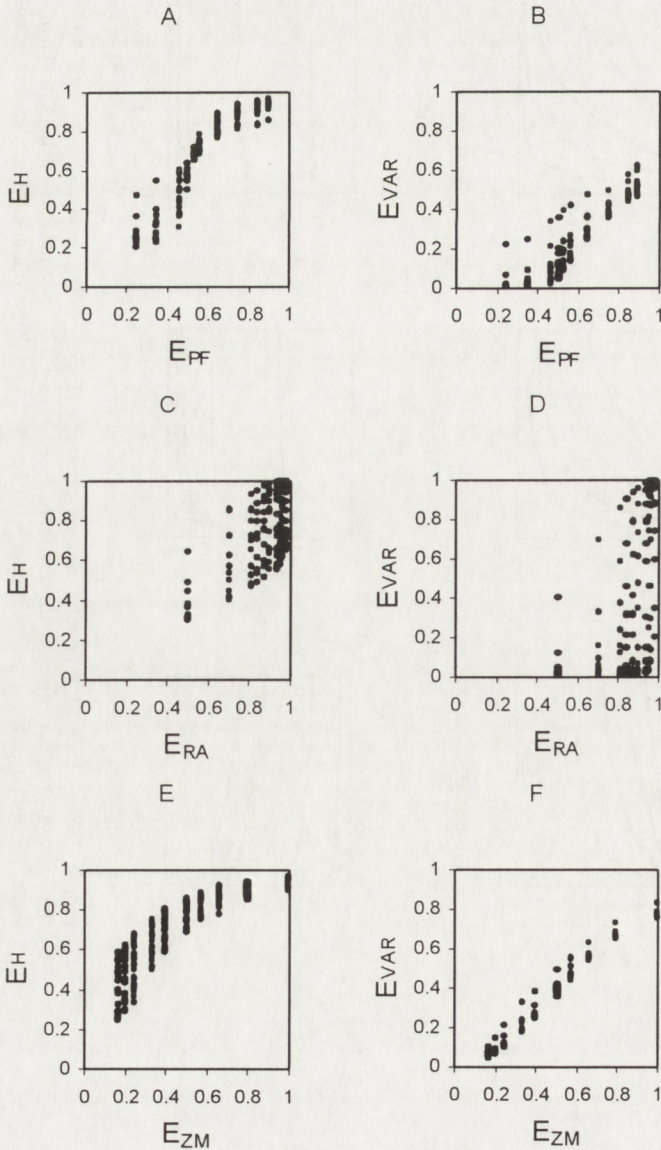


Fig. 8. Dependence of E_H and E_{var} on E_{PF} (A, B), E_{RA} (C, D), and E_{ZM} (E, F). Data from all 510 assemblages described in the methods sections. For definitions of E_{PF} , E_{RA} , and E_{ZM} see equations 12, 14, and 18, respectively.

What are the relationships of these newly defined indices to the classical ones? In the case of the diversity indices Fig. 3 showed the high correlation between the latter and the slope values. Because the new diversity indices all use the negative inverse of the slope the relations between them and the older ones are as close as in Fig. 3. H_H , $H_{1/D}$ or α may further be used as diversity measures. However, this is not the case in the evenness indices. Fig. 8 shows only weak correlations between E_H and E_{var} and E_{PF} , E_{RA} , and E_{ZM} . The fact that these correlations depend on the type of RAD casts further doubts on the applicability of E_H and E_{var} .

3.2. SAMPLING BEHAVIOR OF E_{PF} AND H_{PF}

Any new definition of a diversity statistics has to study the question how the new index depends on species numbers and sample sizes. E_{PF} and H_{PF} have the fortunate feature that we may estimate them independently either by computing the slope of the log abun-

dance – species rank order plot or by fitting the power fraction model to the data set and estimating k directly. The first way is of course the more easier and does not require knowledge of the number of species.

If one uses the slope of the log abundance – species rank order plot both E_{PF} and H_{PF} appeared to be highly dependent on sample size (Fig. 9). In the case of an assemblage following a power fraction model with $k = 0$, H_{PF} may be estimated correctly if at least 35% of the species are represented in the sample, at $k = 0.2$ a sample has to contain at least 60% of the species and at $k = 1.0$ at least 80%. The evenness estimates stemming from these diversity values are either too high or too low depending on the assemblage structure (Fig. 9 A to C). It is therefore difficult to estimate evenness via diversity.

The opposite way, however, gives much better results. Fig. 10 shows fits of a power fraction assemblage at various samples sizes and proves that only 30% of the total species number has to be represented in the sample for a correct estimation of evenness and diversity. It is not necessary to know the total

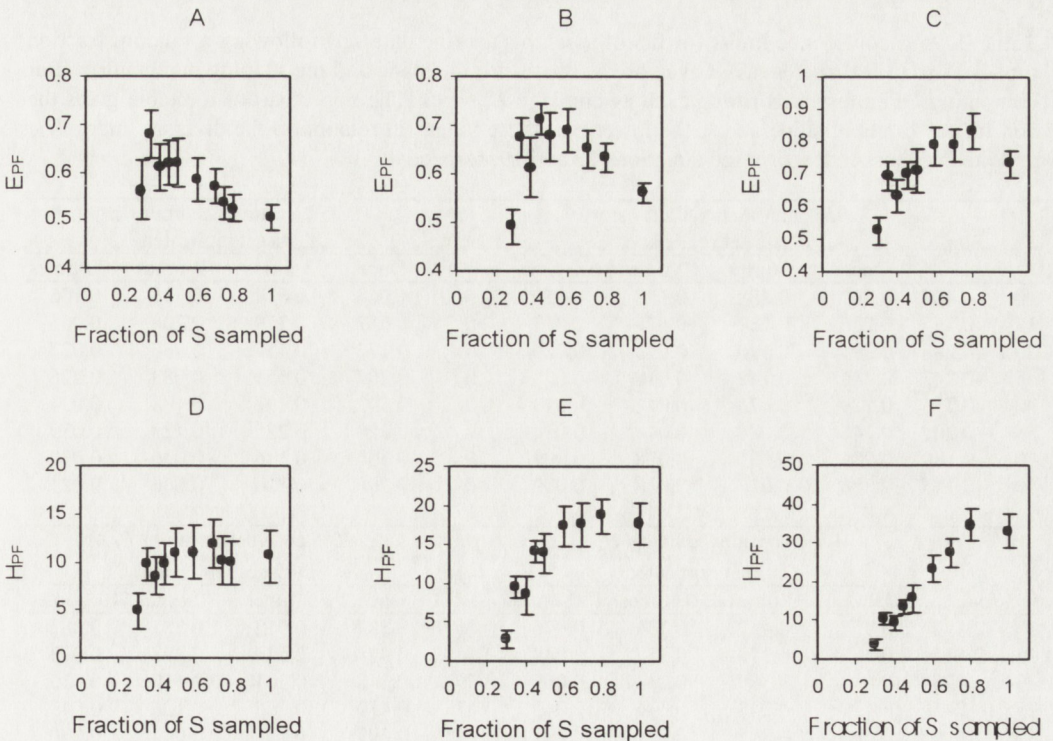


Fig. 9. Dependence of evenness (E_{PF} – equation 18) and diversity (H_{PF} – equation 19) on sample size (fraction of species number S found in the sample) for three power fraction assemblages (100 species) with $k = 0$, (A, D), 0.2 (B, E), and 1.0 (C, F). E_{PF} was in every case computed via the slope using equation 17. The error bars indicate in every case one standard deviation obtained from 20 replicates. The theoretical values of E_{PF} for these assemblages are according to equation 18: 0.5 ($k=0$), 0.56 ($k=0.2$), and 0.75 ($k=1.0$).

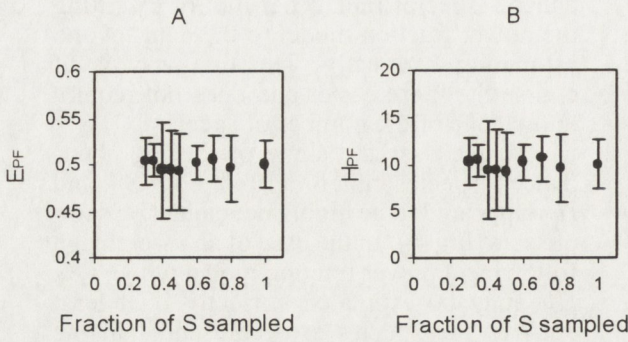


Fig. 10. Dependence of evenness (E_{PF} – equation 18) and diversity (H_{PF} – equation 19) on sample size (fraction of species S found in the sample) for power fraction assemblages (100 species) with $k = 0$. The evenness values were estimated using least square fits of the assemblages as described in part one of this paper (Ulrich 2001). H_{PF} values are computed using equation 20. The error bars indicate in every case one standard deviation obtained from 20 replicates. The theoretical values for such a power fraction assemblage are according to equation 18 and 19: $E_{PF} = 0.5$ and $H_{PF} = 12.5$ (mean slope value of 100 replicates)

number of species in the assemblage (Ulrich in prep.).

How large has the sample to be to reach a good discrimination power? In part one (Ulrich 2001) it was shown that for a sufficiently correct identification of the shaping parameter k the sample has to contain between 200 and 500 times the species number of the assemblage.

It was also shown that it makes few sense to estimate k for assemblages of less than 20 species. Table 2 gives estimates of confi-

dence limits of fits of k and E_{PF} for assemblages of 10 to 50 species. The Table shows that an assemblage size of 20 species indeed marks a boundary because of the step in the confidence limit. Below this species number k – and therefore E_{PF} – have large error terms which in practice make it impossible to discriminate between evenness values from different assemblages. Fig. 11A shows E_{PF} values derived from fits of assemblages from 10 to 50 species and again shows that a step is reached at species numbers above 20. At spe-

Table 2. 95% confidence limits for fits of assemblages (the data set) following a random fraction model of 10 to 50 species (S). Given are estimates for the slope and the shaping parameter k after computing and afterwards fitting each assemblage 20 times. The upper part of the table gives the confidence limits of slope and k , the lower part these values in relation to the diversity index H_{PF} and the evenness index E_{PF} (see equations 18 and 19, respectively)

S	95% confidence limit / slope					k	95% confidence limit / k			
	Slope	Data set replicated					Data set replicated			
		Once	3-times	10-times	100-times		Once	3-times	10-times	100-times
10	-0.404	0.499	0.288	0.158	0.050	0	1.064	0.614	0.336	0.106
15	-0.355	0.226	0.130	0.071	0.023	0	0.657	0.379	0.208	0.066
20	-0.288	0.295	0.170	0.093	0.030	0	0.272	0.157	0.086	0.027
25	-0.243	0.246	0.142	0.078	0.025	0	0.262	0.151	0.083	0.026
30	-0.236	0.129	0.075	0.041	0.013	0	0.342	0.197	0.108	0.034
35	-0.202	0.140	0.081	0.044	0.014	0	0.390	0.225	0.123	0.039
40	-0.180	0.089	0.051	0.028	0.009	0	0.304	0.176	0.096	0.030
50	-0.155	0.088	0.051	0.028	0.009	0	0.208	0.120	0.066	0.021

S	95% confidence limit / H_{PF}					E_{PF}	95% confidence limit / E_{PF}			
	H_{PF}	Data set replicated					Data set replicated			
		Once	3-times	10-times	100-times		Once	3-times	10-times	100-times
10	2.474	0.757	0.437	0.239	0.076	0.469	0.887	0.512	0.281	0.089
15	2.815	0.480	0.277	0.152	0.048	0.447	0.928	0.536	0.293	0.093
20	3.475	0.673	0.389	0.213	0.067	0.507	0.348	0.201	0.110	0.035
25	4.245	0.429	0.248	0.136	0.043	0.478	0.430	0.248	0.136	0.043
30	4.109	0.666	0.385	0.211	0.067	0.485	0.297	0.172	0.094	0.030
35	5.556	0.395	0.228	0.125	0.040	0.497	0.215	0.124	0.068	0.021
40	4.951	0.512	0.295	0.162	0.051	0.487	0.241	0.139	0.076	0.024
50	6.458	0.439	0.254	0.139	0.044	0.488	0.264	0.152	0.083	0.026

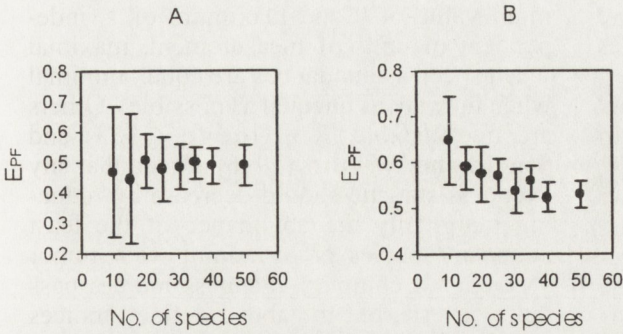


Fig. 11. Dependence of estimates of evenness (E_{PF}) on the number of species in the assemblage for power fraction assemblages with $k = 0$. A: estimates using least square fits of the assemblages as described in part one of this paper (Ulrich 2001b) and using equation 18. B: Estimates obtained by computing the slope and using equation 20. The error bars indicate in every case one standard deviation obtained from 20 replicates. The theoretical value for these power fraction assemblages is according to equation 18: $E_{PF} = 0.5$.

cies numbers above 20 a 95% – confidence of 0.08 (Table 2) for instance means that it would be impossible to discriminate between a random fraction and a canonical log-normal distribution and their associated evenness. Because these fits are obtained using the whole community the associated sample size in this case is 180 times the number of species (it is the quotient of the relative densities of the least and the most abundant species). This is quite a weak discrimination power and shows again how large sample sizes have to be to compute useful evenness values.

For the diversity statistics there is no such sharp boundary in species numbers and the confidence limits given in Table 2 are nearly all higher than in the case of the k – values. That means that the computation of diversities even needs higher sample sizes than of evenness if the diversity is computed via the slope values. If we compute evenness via the slope and use equation 20 than the evenness estimates are clearly species number dependent and good estimates will only be obtained at species numbers above 100 (Fig. 11B).

Important for diversity and evenness statistics are also upper and lower boundaries. Upper and lower boundaries of $-\infty$ and $+\infty$ for diversity and 0 to 1 for evenness values are of course only of theoretical interest. No real community will have such extreme shapes. Even in the most equal distributed community not all species will have the same density but they will have slightly different densities stemming from statistical noise. Their distribution will therefore follow a Poisson distribution. Such a distribution will have a slope of $-2/S$ and therefore a maximal diversity of

$$H_{max} = S / 2. \quad (21)$$

This results in a maximum evenness of 0.992 for the power fraction and of 0.998 for

the random assortment type of distribution. A Zipf-Mandelbrot distribution has a maximum evenness of 1 at $k = 1$.

Minimum possible diversity values depend on the minimum possible density in a community. If the species of a community fill the whole density range from maximum to minimum possible density then the minimum diversity is the negative inverse of the slope of the linear regression between maximum and minimum density. This slope value is of course $\ln(D_{min}) / S$, where D_{min} is the minimum possible relative density. The minimum possible diversity value is therefore

$$H_{min} = S / -\ln(D_{min}) \quad (22)$$

If for, instance, the maximum possible density in a community of 50 species is 100 individuals / ha and the minimum possible density 1 individual / ha then $H_{min} = 50 / -\ln(0.0001/100) = 3.62$. The associated evenness of this example will be according to equation 17 $E_{min} = 0.42$.

4. DISCUSSION

The above results show how the current confusion about the use of evenness indices stems from the ambiguities in defining evenness. Definitions stemming from basic features of relative abundance distributions may help to clarify the concepts of evenness and diversity.

The above equations define diversity and evenness for three types of relative abundance distributions, a power fraction, a random assortment, and a Zipf-Mandelbrot type. Zipf-Mandelbrot type distributions are only seldom encountered in nature and it may be that existing examples all stem from truncated power fraction types (Frontier 1985). Random assortment type distributions are

frequently encountered in samples and were indeed originally (as geometric or log-series distributions) intended to describe samples. Only species poor, early successional or not fully censured communities are thought to follow this type of RAD (Whittaker 1972, Pielou 1977, Tokeshi 1993). The latter author rightly remarks that fit of a random assortment type distribution may only be the result of too few data points giving the impression of a linear sequence. Reanalysis of existing claims also point to this interpretation (Ulrich unpubl.).

The power fraction model of Tokeshi (1996) has the very attractive feature that it can encompass many of the so far described RAD models by changing one shaping parameter (Ulrich 2001b). For k -values below -0.1 it takes a nearly linear shape in a log abundance – species rank order plot similar to random assortment, geometric or log-series models. It is therefore an ideal model to describe the whole range of shapes by a single parameter and it would be very worthwhile to reanalyze existing data whether they can be described by this model. Preliminary surveys suggest such a possibility (Ulrich unpubl.). The model may then serve as a standard for diversity and evenness measures.

What are the properties of the above defined evenness and diversity indices? An important property of diversity indices is that they should be strictly additive that means that the total diversity in a pooled set of communities should be greater than the diversity within the communities (Lewontin 1972, Lande 1996). All three proposed diversity measures pass this criterion. This feature also allows to separate α , β , and γ diversity (Whittaker 1972).

Evenness is always derived from the shaping parameter k of a distribution. All distributions with the same parameter values have by definition the same evenness. At first glance, this is may be counterintuitive in the case of communities following Zipf-Mandelbrot RADs. However, this stems only from the common way of plotting distributions. Taking a double log plot makes this definition the natural way but astonish us in other RADs.

Routledge (1983) and Smith and Wilson (1996) listed a number of properties every evenness index must have. Some of these criteria are trivial and of course met by the above defined evenness indices (mini-

um value of 0 and maximum of 1, independent of units of measurement, maximal when species abundances are equal, minimal when they are as unequal as possible). Others are questionable. Routledge (1983) and Smith and Wilson (1996) argued that any evenness statistic should decrease by reducing marginally the abundance of the least abundant species or by adding very minor species. All common evenness indices pass these criteria, but the above defined indices not. However, such a concept stems from a very static view of communities. Imagine a community following a canonical log-normal distribution. The most minor species live always in danger of going extinct and random or seasonal fluctuations of the extinction level leads to fluctuations in species numbers. For insect communities these yearly species turnover rates are frequently in the order of 5 to 20% per year (Den Boer 1985, Dempster *et al.* 1995, Ulrich 1999b). Such fluctuations however do not change the resource apportionment and the relative abundance distributions. The community will furthermore be divided according to a canonical log-normal and it seems logical to describe it with the same evenness value. The changes in species numbers are described by varying slopes and therefore diversities.

Another questionable criterion is symmetry (Pielou 1977, Smith and Wilson 1996). According to common interpretation of evenness a density sequence 1000, 1000, 1000, 1 should have the same evenness than 1000, 1, 1, 1. E_{var} and E_Q pass this criterion other indices not and the above defined evenness indices do also not. Both sequences clearly follow different relative abundance distributions. The first equals more a MacArthur fraction model (Tokeshi 1990), the latter may stem from a Zipf-Mandelbrot division procedure. It is not possible to compare both sequences directly but if we accept a power fraction model as the universal standard then the first sequence has clearly a higher evenness than the latter ($k = 0.75$ and 0.06).

Smith and Wilson (1996) also identified a good mid range behavior of an evenness index as a desirable feature. These authors favored a density sequence of 800, 600, 400, and 200 as being intermediate. Such a view cannot be accepted because intermediate has to be defined in terms of real community structures but not of arbitrary densities. We have to construct an appropri-

ate null model, a randomly constructed community. Such a community should have an evenness value around 0.5. May (1975) favored the canonical log-normal because of its derivation from the central limit theorem. Tokeshi (1993), on the other hand, pointed to a random assortment model (with $k = 1$), because it can be considered similar to the neutral model approach of Caswell (1976). From the definition of equation 12 we see that a random assortment model with $k = 1$ has an evenness value of 0.5, a very desirable feature. Equation 17 gives a canonical log-normal the evenness 0.52. Of course, both values can only be interpreted in terms of their underlying RADs and cannot be compared directly. A third candidate for an appropriate null model of a relative abundance distribution is the random fraction model of Tokeshi (1990), a model in which all niche divisions occur at random. Such a model has (according to equation 18) an evenness of exactly 0.5. It should however be noticed that in real communities evenness values less than 0.4 (equivalent to k -values less than -0.3) will seldom be encountered (Sugihara 1980, Tokeshi 1996, Ulrich unpubl.).

In Figs 9 to 11 and Table 2 it was shown that it makes few sense to compute evenness and diversity for communities with less than 20 species because of the high variance of this estimate. Fig. 9 also shows the dependence of H_{PF} on sample size. This dependence will be especially pronounced in small communities. This finding has implications for all diversity statistics and studies in which diversity is used for comparison. Recently the stability – diversity debate gained much interest (Naeem *et al.* 1994, 1995, Tilman 1996, 1999, Naeem and Li 1997, Doak *et al.* 1998, Tilman *et al.* 1998, Sankaran and McNaughton 1999) although there is little concern how to measure stability, evenness and diversity (Doak *et al.* 1998). Diversity is most often defined as species richness. The above results indicate that this may be the best way in small communities where the species number is known. In medium sized and large communities the species numbers may fluctuate considerably and are often unknown. Because the estimation of diversities via the slope value requires no knowledge of the total number of species indices as the ones developed above seem to be more appropriate in the latter cases.

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5. SUMMARY

The recent concepts of diversity and evenness and their definitions are discussed. On the basis of 510 model assemblages of different species numbers and structures (Table 1) it is shown that especially the ambiguities in defining evenness has led to confusion about evenness measures and their applicability (Figs 1, 2, 3, 4, 5, 6). Definitions of diversity and evenness from parameters of relative abundance distributions (Figs 7, 8) avoid such ambiguities. In this paper diversity is defined as the negative inverse of the slope of the relative abundance distributions and evenness is the arcus tangens transformed shaping parameter. Diversity and evenness depend therefore on the type of relative abundance distribution and diversities from communities of different types of relative abundance distributions (power fraction, random assortment or Zipf-Mandelbrot type) cannot be compared directly. The properties of these newly defined diversity and evenness indices and their behavior in samples (Figs 9, 10, 11, Table 2) are discussed and it is shown that existing tests contain in part inappropriate features. It is also shown that Tokeshi's newly developed power fraction model may serve as a universal basis for defining diversity and evenness indices.

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