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## SPECIES AREA RELATIONS GENERATED BY THEORETICAL RELATIVE ABUNDANCE DISTRIBUTIONS: PARAMETER VALUES, MODEL FIT AND RELATION TO SPECIES SATURATION STUDIES

**ABSTRACT:** Using model assemblages and random samplings the relations between 8 relative abundance distributions (RADs) (broken stick, log-series, power fraction, random fraction, Sugihara fraction, and two types of Zipf-Mandelbrot models) and resulting species-area relationships (SPARs) were studied. It is shown that the model fit of the power function and the exponential SPAR model depends mainly on the number of species per unit of area, the fraction of singletons in the sample, and the total species number in the assemblage. Sugihara and power fraction RADs did not necessarily led to power function SPARs but are characterized by relatively high slope values in comparison to other distributions. Random placement and sampling of individuals of Zipf-Mandelbrot and log-series distributions resulted in curvilinear local vs. regional plots and the slope value  $z$  of the power function SPAR was not necessarily constant but could be forced to become constant by introducing a correction factor into the power function SPAR. The implications of these findings for detecting local species saturation are discussed.

**KEY WORDS:** relative abundance distribution, species-area relation, species saturation, proportional sampling, power fraction, Zipf-Mandelbrot distribution, log-series, Sugihara fraction, random fraction

### 1. INTRODUCTION

Although the basic concepts of species-area relationships (SPARs) stem from the beginning of the century, models and applications of these relations are still one of the main subjects of interest of current community ecology (Rosenzweig 1995, 1999, Williams 1995, Harte and Kinzig 1997, Harte *et al.* 1999, Ulrich 2000a, b, c).

Ulrich (2000a, b, c) used model assemblages (in this paper assemblage is used in favor of community to express that there are no interactions between the model species) to study model fit and parameter values of the power function and the exponential SPAR model described by

$$S_a = S_{unit} A^z, \quad (1)$$

and

$$S_a = b \ln(A) + S_{unit} \quad (2)$$

where  $S_a$  is the number of species in area  $A$ ,  $S_{unit}$  the number of species per unit of area (the intercept of the  $S_a$ - $A$  plots), and  $b$  and  $z$  the factor and the slope of the models (Connor and McCoy 1979).



The present study continues this work on both SPAR models but focuses on theoretical relative abundance distributions (RADs). Plenty of RAD-models have been proposed to describe and explain the rank abundance plots of plant and animal communities (Fig. 1). These models are either distribution orientated (e.g.: geometric, log-series, log-normal, Zipf-Mandelbrot) or stochastic (e.g.: sequential breakage model, power fraction, random fraction) and most of the distribution orientated models have their stochastic counterparts (Tokeshi 1990, 1993, 1996).

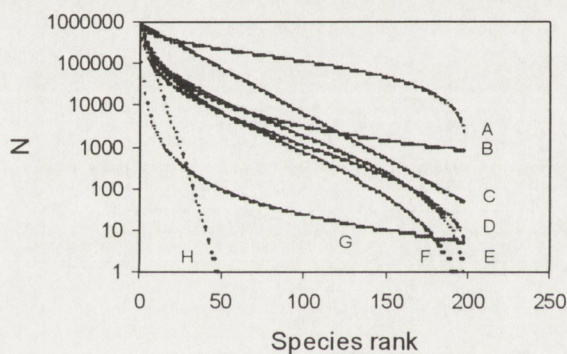


Fig. 1. Eight relative abundance distributions studied in this paper. A: broken stick, B: Zipf-Mandelbrot 1 (with parameters  $k = 2$  and  $X = 5$ ), C: log-series (with slope = 0.05), D: Sugihara fraction (fixed breakage probability of 0.75), E: power fraction with exponent  $k = 0.05$ , F: random fraction, G: Zipf-Mandelbrot 2 (with parameters  $k = 2$  and  $X = -0.5$ ), H: geometric (with  $k = 0.25$ ).

It is generally assumed that log-series distributions lead to exponential species-area relationships, whereas log-normal distributions generate power function SPARs (Fisher *et al.* 1943, May 1975, Sugihara 1981). For the broken stick model May (1975) also expected a better fit of the power function model. However, He and Legendre (1996) argued that irrespective of community structure but depending on sample size both models may be applicable and several models predict power function SPARs without referring to underlying community structures (Wissel and Maier 1992, Harte *et al.* 1999, Ney-Nifle and Mangel 1999). Ulrich (2000a) showed that model fit depends mainly on the number of singletons in the sample (the number of species found only once) and that, irrespective of underly-

ing RAD, all mechanisms influencing this number will also influence model choice.

Plots of regional vs. local species numbers are one of the main tools to infer local species saturation (Terborgh and Faaborg 1980, Cornell 1985, Lawton 1990, Cornell and Lawton 1992, Cresswell *et al.* 1995, Caley 1997, Caley and Schluter 1997) (Fig. 2). If such plots result in a constant proportion of local to regional numbers the local communities are assumed to be unsaturated with species (cases A and B in Fig. 2). Curvilinearity or a constant local species number indicates local saturation (cases C and D in Fig. 2) (Cornell 1985).

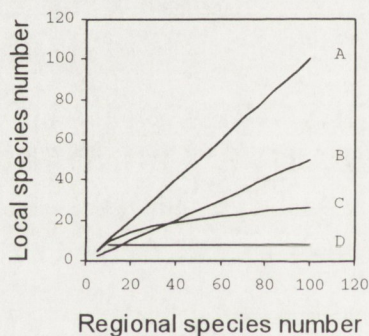


Fig. 2. Four models describing the relationship between local and regional number of species. A: all species of the regional species pool are found on the local scale; B: proportional sampling, there is a fixed ratio between local and regional species number; C and D: local communities are saturated with species.

Alternatively, the slope  $z$  of the power function SPAR may be used to infer local saturation (Westoby 1993, Srivastava 1999, Ulrich 2000b). Simple rearrangement of equation (1) results in

$$z = -\frac{1}{\ln(A)} \ln \frac{S_{unit}}{S_a} \quad (3)$$

If  $S_a$  is interpreted as the regional and  $S_{unit}$  as the local species numbers  $z$  remains constant if the proportion between  $S_{unit}$  and  $S_a$  is constant. A constant  $z$  indicates therefore local unsaturation. Local saturation results in a rising slope  $z$ . Both methods of detecting species saturation are therefore closely related and this is the reason why they are treated together in this paper.

The interpretation of curvilinearity in a plot of regional vs. local species numbers as an indication of local saturation relies on the



assumption that a null model assuming a random distribution of the individuals of all species in a given area  $A$  will always result in a so-called proportional sampling. That means the relation between  $S_{unit}$  and  $S_a$  will be the same at all spatial scales (Caley and Schluter 1997). An additional assumption is that the relative abundance distributions are the same at the regional and the local scale.

Caley and Schluter (1997) were the first to assume that certain RADs may not result in proportional sampling. They studied log-normal models and found that at small local sample sizes (below 200 times the regional species number) proportionality is violated. Hawkins and Compton (1992) assumed the same under the special case that the sample size is small and held constant irrespective of region size (resulting in a lower detection probability of rare species). Ulrich (2000b), on the other hand, did not find deviations from proportionality when studying various model assemblages.

The aim of the present work is to study the relation between relative abundance distributions and resulting species area relationships and to assess under which conditions the slope  $z$  of the power function SPAR model and the intercept  $S_{unit}$  can be used to infer local species saturation.

## 2. MATERIALS AND METHODS

For the present study eight RAD models were selected which span the whole range of different shapes. These models are the geometric model (further termed as geo), the log-series (lser), two forms of Zipf-Mandelbrot distributions (zipf1, zipf2), the random fraction model (ranf), the Sugihara fraction (sug) (the stochastic counterpart of the canonical log-normal distribution), a power fraction model (pow), and the broken stick model (bro). The properties and generation procedures of these models are described elsewhere in detail (Preston 1962, Pielou 1977, Sugihara 1980, Frontier 1985, Gray 1987, Tokeshi 1990, 1993, 1996) and need not be repeated again. Figure 1 shows these distributions for 200 species each. Each of the above RADs (with the same parameter settings as in Fig. 1) was computed for 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 120, 140, 160, 180, and 200 species (geometric 10, 20, 30, 40, 48 species) resulting in a total of 110 distributions.

In the next step the individuals of these assemblages with the distributions described above were placed at random into the cells of a  $300 \times 300$  cell grid. For this placing procedure arbitrary densities of 900 000 and 90 000 individuals for the most abundant species of each assemblage were used resulting in 220 grids with mean densities of 10 and 1 individuals per cell for the most abundant species and a max. density difference from the most abundant to the least abundant species of  $9 \times 10^4$  and  $9 \times 10^5$ . Afterwards 100 cells of each grid were chosen at random and the number of species and of individuals of each species counted. Placing and sampling was done with the FORTRAN program *Community Model* which is described in detail in Ulrich (1999, 2000a). Species-area plots were computed using a sequential adding of the species numbers of these 100 cells (Ulrich 2000a). Because all species per cell were sampled no effect of small sample sizes influenced the results (Caley and Schluter 1997).

Species area relationships computed by such a process are highly susceptible to the ordering of cells. The ordering of cells was therefore reshuffled 20 times at random (according to the procedure of Colwell and Coddington 1994) and the SPARs and the parameters given below are computed using the resulting mean species numbers per cell.

For each of these assemblages the following parameters were computed: number of species in the assemblage  $S_a$ , absolute species density  $S_{unit}$  (number of species per cell), the relative species density  $S_{unit}/S_a$ , number of species sampled  $S_s$  and fraction of total species number sampled ( $S_s/S_a$ ), number of species found in only one cell (singletons), relative number of singletons (singletons/ $S_s$ ), and Shannon-indices of diversity and evenness (whole assemblage and sample separately). As a descriptor of the relative abundance distributions of the assemblages and the samples the standard deviation of  $\log_2$  (densities) (SD) – also termed Gaussian width – was used (Sugihara 1980, Tokeshi 1993, 1996).

## 3. RESULTS

### 3.1. MODEL FIT

Ulrich (2000a) showed that the main factor influencing the fit of the power func-



tion or the exponential model of species-area relationships (measured by the variance explanation  $R^2$ ) is the fraction of singletons in the sample. This holds also when using theoretical RADs (Fig. 3A). Both models show a characteristic pattern when plotting model fit against fraction of singletons in the sample. The power function model fits best if more than 30% of the species were found only once; the exponential model performs best at fractions of 5 to 30% singletons. In the range between 25 and 35% singletons both models performed nearly equally well. If nearly all species are found more than once (fraction of singletons less than 5%) both models performed worse, mainly due to the fact that the resulting SPARs had a very flat appearance.

The above pattern is better seen when plotting the difference in variance explanation ( $R^2$  of exponential model –  $R^2$  of power

function) of both models against the fraction of singletons. (Fig. 3B) This results in a linear relationship between the difference in  $R^2$  and the fraction of singletons. The plot gives the same point of switching between both models as derived in Ulrich (2000a): 30%. The good linear regression shown in Figure 3B also proves that the type of RAD has only a minor importance for the fit of one or both models (power function or exponential).

The above pattern is independent of the slope of the SPARs. This is seen when using the slope  $z$  of the power function model as an estimate of this slope (Fig. 4). Both models showed the same trend in performance: steadily rising  $R^2$ -values until a slope of 0.5 is reached. At higher slope values the performance of the exponential model slightly decreased.

Different RADs result in different fractions of singletons and different slopes of SPARs. Model fit should therefore be influenced by the underlying RAD model. From Figure 5 three different patterns may be inferred. The geometric, log-series and also the broken stick RADs [which all have a linear or – in the case of the broken stick – nearly linear appearance in a density-rank order plot (models A, C, and H in Fig. 1)] were always better fitted by the exponential SPAR model (although for geo and lser the differences are small for higher species numbers). In the case of the S-shaped power-, random-, and Sugihara fraction RADs (model D, E, and F in Fig. 1) as well as for zipf1 (model B in Fig. 1) model fit proved to be dependent on the number of species. At lower species numbers (below 100 species) the exponential model fitted better (in 24 out of 30 assemblages), at higher species numbers the power function gave better results (11 out of 15 assemblages). The point of switch lies around 100 to 120 species. The last case is represented by the zipf2 RAD (model G in Fig. 1). The power function SPAR-model fitted nearly always better irrespective of the number of species.

The observed switching point in the case of the sug, pow, ranf and zipf1 models, of course, depends on the parameter settings of the assemblages, especially on the maximal density per cell. At a maximal density per species of 10 ind. per cell the general pattern of Figure 5 remained the same for sug, pow, and ranf but the switching point changed to around 250 species. In the case of zipf1, however, the power function fitted better at species numbers above 90 (data not shown).

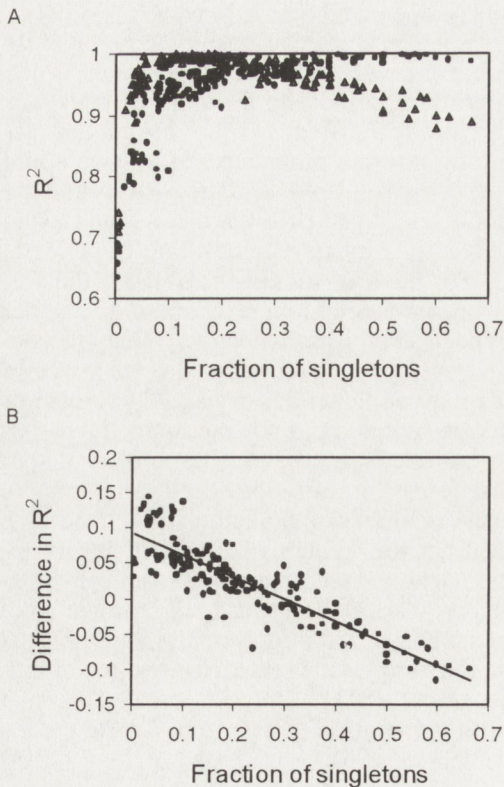


Fig. 3. Model fit of the power function and the exponential model of species-area relationships depending on the fraction of singletons in the sample. Data of all assemblages generated. A: Variance explanation  $R^2$  of the exponential (triangle) and the power function model (circle). B: Difference of  $R^2$  (exponential minus power function) depending on the fraction of singletons.



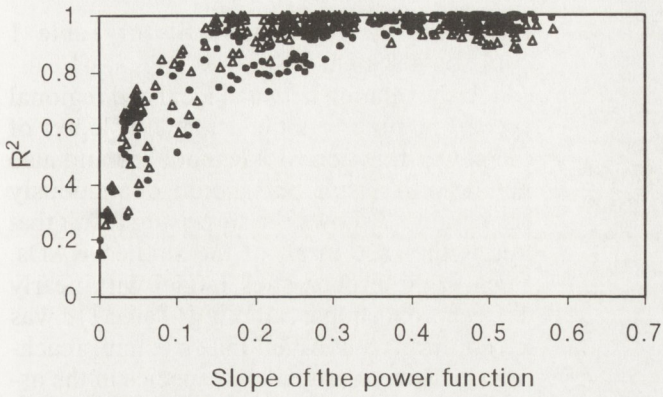


Fig. 4. Model fit of the power function and the exponential model of species-areas relationships depending on the slope of the power function. Data of all assemblages generated. A: Variance explanation  $R^2$  of the exponential (triangle) and the power function model (circle).

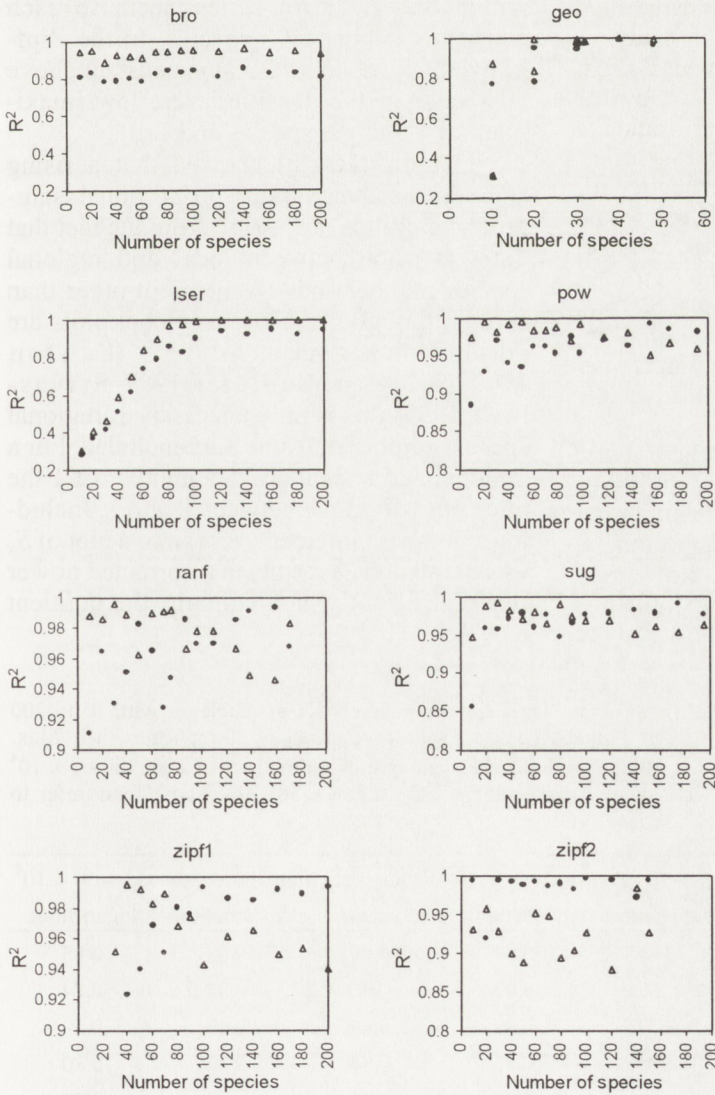


Fig. 5. Dependence of model fit (variance explanation  $R^2$ ) of the exponential (triangle) and the power function model (circle) on species number for eight different RADs. Data for assemblages with max. density difference of  $10^4$ .



### 3.2 REGIONAL VS. LOCAL SPECIES NUMBERS

The relationship between local and regional diversity was studied using plots between the number of species per cell (local) and the species number of the whole assemblage (regional). From the 8 tested RAD models only in the case of the broken stick, the random fraction and the power fraction (with parameter  $k = 0.05$ ) model regressions between local versus regional species number resulted in best fits of linear regressions (Table 1) indicating proportional sampling. This result was independent of the number of individuals per cell and the total number of individuals of the whole community. The Sugihara fraction showed a slight tendency to curvilinearity expressed by the nearly identical fits of the logarithmic and the linear regression in Table 1. The log-series, geometric, and zipf1 models were better fitted by a logarithmic regression (Table 1) and showed a clear curvilinear pattern even resulting in asymptotic behavior (Fig. 6). Zipf2, the model with the highest number of rare species, did not result in any correlation between  $S_{unit}$  and  $S_a$ ; in this case the local species numbers were nearly identical over the whole range of regional numbers.

The latter point indicates that the fraction of rare species (measured by the number of singletons) may influence the relation between local and regional species numbers. This, however, was not the case. No regression between the mean fraction of singletons of each of the models and the  $R^2$ -values of the

linear and the logarithmic fits of Table 1 could be detected.

If the relation between local and regional species number is not constant the slope  $z$  of the power function SPAR model should also not be a constant but should continuously rise. Figure 7 shows the surprising result that this is the case in all of the studied RADs. Even in the broken stick model with nearly perfect proportional sampling (Table 1)  $z$  was by no means a constant but rose until reaching a plateau at around 100 species in the assemblage. Such a plateau at around 100 species also occurred in the sug, pow, and ranf models. In the log-series  $z$  seems to reach constancy beyond 200 species. In the Zipf-Mandelbrot models  $z$  became constant above 50 species if the densities were low (maximum of 1 ind. per species and cell).

Ulrich (2000b) showed that a rising slope value even under proportional sampling conditions may result from the fact that the regression between local and regional species numbers has an intercept other than zero. Although most local/regional plots are drawn with intercepts of zero (Lawton 1990, Caley and Schluter 1997, Srivastava 1999) this is only necessary if regional species number of 0 and 1 are included. For a regional and a local species number of 1 the intercept will range between 0 and 1. Including a non-zero intercept (icpt) into a plot of  $S_a$  vs.  $z$  (equation 3) results in a corrected power function SPAR which contains the quotient  $icpt/S_a$ :

Table 1. Local (one cell) versus regional (total assemblage) species numbers for assemblages with 10 to 200 species and 8 different relative abundance distributions. The  $R^2$  - values are means of 20 replicates each. Max. dd - max. density difference between the most and the least abundant species. In the case of max. dd =  $9 \times 10^4$  the geometric distribution had only 4 data points (max. number of species = 38). Bold type fonts refer to regression models of best fit.

Model	Fit of regression ( $R^2$ ); max. dd = $9 \times 10^5$			Fit of regression ( $R^2$ ); max. dd = $9 \times 10^4$		
	linear	exponential	logarithmic	linear	exponential	logarithmic
Broken stick	<b>0.99</b>	0.85	0.87	<b>0.99</b>	0.88	0.85
Log-series	0.63	0.50	<b>0.93</b>	0.40	0.34	<b>0.74</b>
Sugihara fraction	0.86	0.79	<b>0.89</b>	<b>0.60</b>	0.59	0.59
Random fraction	<b>0.88</b>	0.85	0.82	<b>0.84</b>	0.82	0.80
Power fraction	<b>0.93</b>	0.84	0.88	<b>0.81</b>	0.78	0.72
Geometric	0.89	0.86	<b>0.96</b>			
Zipf Mandelbrot 1	0.53	0.45	<b>0.86</b>	0.40	0.54	<b>0.67</b>
Zipf Mandelbrot 2	0.07	0.07	0.08	0.01	0.00	0.00



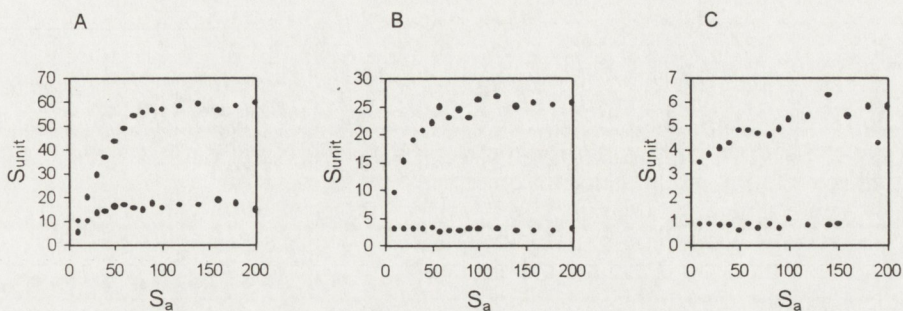


Fig. 6. Local ( $S_{unit}$ ) and regional ( $S_a$ ) species numbers of the log-series (A), the zipf1 (B), and zipf2 (C) model for species numbers ( $S_a$ ) between 10 and 200 species. Upper data points: assemblages with a max. density difference of  $10^5$ , lower data points: max. density difference of  $10^4$ .

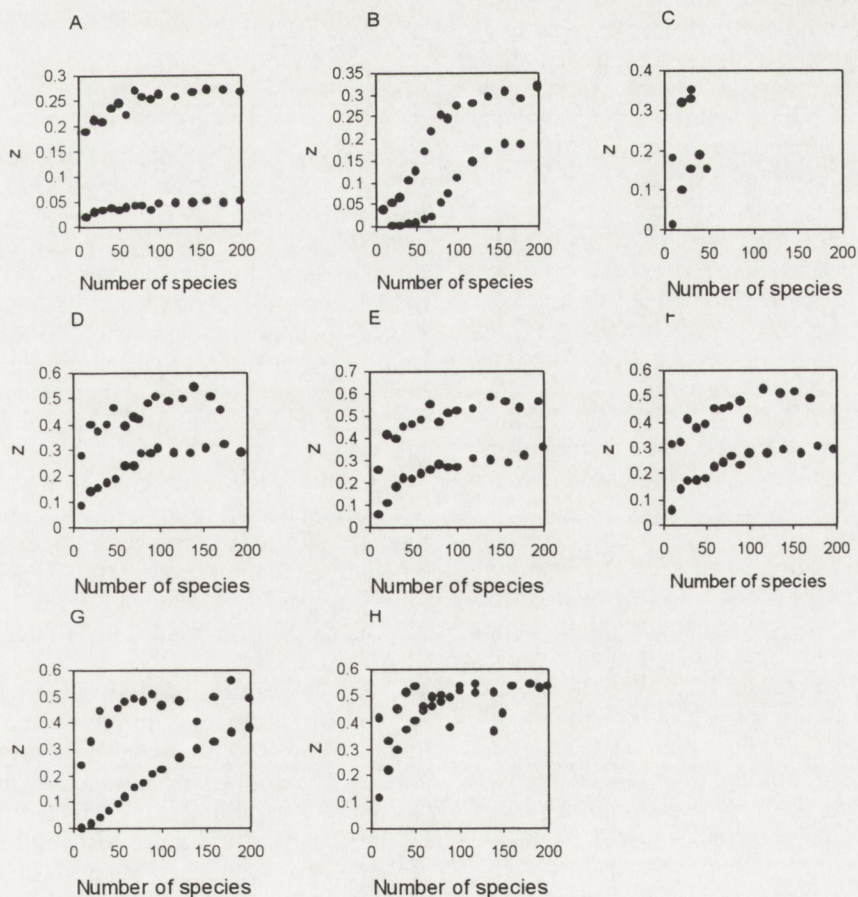


Fig. 7. Slope value  $z$  of the power function SPAR model depending on the number of species of the assemblages. A: bro, B: lser, C: geo, D: ranf, E: sug, F: pow, G: zipf1, H: zipf2. Upper data points from assemblages with a max. density difference of  $10^4$ , lower data points from a max. density difference of  $10^5$ . In the case of geo the max. number of species was 48 (max. density difference of  $10^5$ ) and 38 (max. density difference of  $10^4$ ), respectively.



$$z = -\frac{1}{\ln(A)} \ln\left(\frac{S_{unit}}{S_a} - \frac{icpt}{S_a}\right) \quad (4)$$

This correction resulted in the broken stick, the power fraction, the random fraction and the Sugihara fraction model in a constant slope value  $z$  (with a moderate variance) except for the lowest species numbers (10 to 40) (Fig. 8). The corrected slope values are in every case higher than the original ones. For the distributions without proportional sampling this method, of course, did not result in a constant slope.

#### 4. DISCUSSION

The above results confirm the findings of (Ulrich 2000a, b c) that a given relative abundance distribution not unambiguously leads to a special type of species-area relationship but that sampling method, densities, and species numbers to a large extent influence the model fit. For the present analysis the sampling procedures were held constant to study the importance of density (ind. per cells) and species numbers.

The higher the species density (the number of species per cell) in relation to the total species number, the better was the fit of the exponential model. Such a density dependence of model fit has also been found by Ney-Nifle and Mangel (1999). Increasing the species number ( $S_a$ ) of the assemblage (which in the models used simultaneously enhanced the density per cell) increased in most models also the species density ( $S_{unit}$ ) of a factor lower than 1 (max. 0.62 in the broken stick distribution) (Table 1 and Fig. 7). However, there was always a positive intercept of the  $S_{unit}$ - $S_a$  plot which caused lower relative species densities ( $= S_{unit}/S_a$ ) at higher species numbers. This resulted in higher slopes and better fits of the power function model (Fig. 8).

How to interpret positive intercepts? Such intercepts are artifacts stemming from the regression procedure because at very low regional species numbers the linearity will necessarily be violated or, in other words, such species numbers lie outside the range of the regression (Cornell and Lawton 1992, Cresswell *et al.* 1995). Nevertheless, non-zero intercepts have to be considered when restating local-regional plots in terms of species-area relationships. When construct-

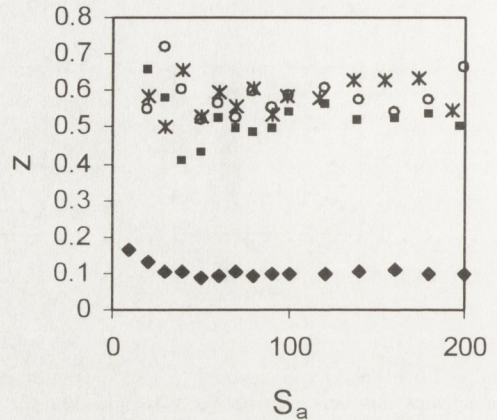


Fig. 8. Slope  $z$  of the power function model in relation to the number of species  $S_a$  of the assemblage after correcting the power function SPAR for a non-zero intercept (according to equation 4). quadrate – power fraction, romb – broken stick, circle – Sugihara fraction, star – random fraction.

ing such plots the regressions may not be forced to go through the origin as has been done in several studies (Hugueny and Paugy 1995, Hugueny *et al.* 1997, Caley and Schluter 1997). Only Cresswell *et al.* (1995) considered non-zero intercepts when drawing local-regional plots. Their test of detecting the dependence of local on regional species numbers (excluding the local number from the regional and then regressing) leads quantitatively to the same results as introducing the correction factor proposed in this study.

Contrary to the popular view a canonical log-normal distribution (equivalent to a Sugihara fraction) does not necessarily imply a better fit of the power function SPAR model (as shown in Figs 2 and 4) but the log-series did nearly always result in an exponential SPAR model.

Power fraction models (into which the Sugihara fraction and the log-normal can be included) are characterized by a higher proportion of middle ranging species, but relatively few very abundant or very rare species. Figure 9 shows that these distributions have higher slope values than other, more equal or more unequal, distributions. Such high slope values have previously been assumed by Leitner and Rosenzweig (1997) for the log-normal but not related to other types of RADs. The findings are also in line with the result of Ulrich (2000b) who showed that RADs with SD values between 2 and 4 [the



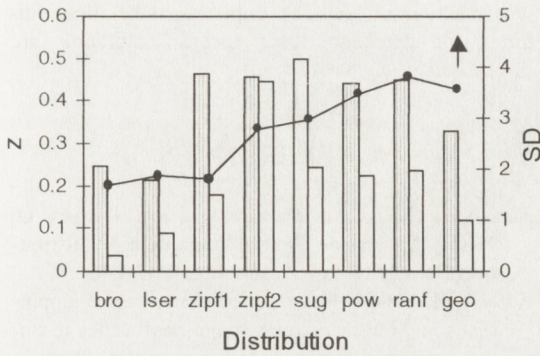


Fig. 9. Slope values  $z$  of the power function SPAR model and the standard deviation of  $\log_2$  densities (SD) of 8 different theoretical relative abundance distributions with 200 species. Scattered bars: slopes at a max. density difference of  $10^4$ , white bars: slopes at a max. density difference of  $10^5$  (both left axis). Data points refer to the SD values (right axis). The SD value of the geometric distribution refers only to an assemblage of 48 species. For higher species numbers this SD values would be much higher (indicated by the arrow).

range where assemblages fitted by power fraction models frequently lie (Tokeshi 1996)] have the relatively highest slopes. The results do not support the view of constant slope values around 0.25 for the canonical log-normal.

Zipf-Mandelbrot models which are characterized by a high number of rare species have largely been neglected in the ecological literature (e.g. Tokeshi 1990, 1993), although especially marine animal assemblages seem frequently to follow these types of distributions (Amanieu *et al.* 1981, Frontier 1985, Wilson *et al.* 1998). They seem also to be applicable in large samples where the rarest species are missing (Wilson 1991, Ulrich unpubl.). It is shown that Zipf-Mandelbrot models will frequently generate power function SPARs with comparably high slopes values.

Plots between local and regional species numbers are a new and often used tool to infer local species saturation. The recent review of Srivastava (1999) lists 36 papers using the method. All of them rely on the assumption that local and regional relative abundance distributions do not differ significantly and that in unsaturated communities higher regional species numbers result in proportionally higher local numbers. Non-proportional sampling, resulting in curvilinear plots of local vs. regional species numbers, are taken as

an indication for local species saturation (Cornell 1985, Lawton 1990).

The first assumption has to be tested in real communities and lies outside the scope of the present paper. The second assumption was tested in this paper and it was shown that relative abundance distributions which produce a high proportion of rare species do not exhibit a proportional sampling pattern. Log-series and Zipf-Mandelbrot distributions resulted in curvilinear local – regional plots even under random placement and sampling conditions. In the Sugihara fraction models (similar to the log-normal) a slight tendency to curvilinearity was detected. The relative abundance distribution has therefore to be taken into account when interpreting local vs. regional plots. Even strong deviations from linearity do not necessarily indicate local saturation but may stem from samplings out of relative abundance distributions with higher fractions of rare species at the regional scale.

Recently, Caley and Schluter (1997) found that small sample sizes may also result in deviations from proportionality and Griffiths (1997) suggested that different body size distributions at the regional scale may effect the detection probability and result in a bias towards curvilinearity. Srivastava (1999) especially focused on differences in regional size, habitat type and pseudoreplication as misleading factors. All of these factors were excluded in the present study. Cells were sampled quantitatively, scales (areas sampled) were held constant, heterogeneity and aggregation of species not included and pseudoreplication could not occur. The found deviations from proportionality are therefore not the result of the sampling procedures but are intrinsic features of certain relative abundance distributions.

In this respect, curvilinear local-regional plots resulting from underlying log-series distributions deserve attention. Such distributions are often found in small or early successional communities (Bazzaz 1975, Pielou 1977, Tokeshi 1993) or in communities insufficiently sampled (Tokeshi 1993) and some of the studies reporting species saturation also dealt with such small communities (Aho 1990, Tonn *et al.* 1990, Aho and Bush 1993, Kennedy and Guégan 1994). It seems to me that the interpretation of saturation in these studies is not reliable until a sound analysis of the relative abundance patterns of the communities has been under-



taken. Analyses of small communities may suffer from high stochastic effects and the above results indicate that the regional communities should have at least 20 species to exclude these effects. Because most studies claiming evidence for local saturation have also been criticized for being pseudoreplicated (Srivastava 1999) or not considering habitat variation (Caley and Schluter 1997) the above argumentation adds further doubts whether local species saturation has up to now really been found.

Because of the close relation between local and regional species numbers and the slope parameter  $z$  of the power function SPAR, non-constancy of the latter was also used to infer species saturation (Westoby 1993, Srivastava 1999). The above results showed that even under proportional sampling  $z$  is not constant at low species numbers (below 20) and that a non-zero intercept of the local-regional plot has to be included as a correction factor. Otherwise, use of  $z$  to infer species saturation may be highly misleading.

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## 5. SUMMARY

Using model assemblages and random samplings the relations between 8 relative abundance distributions (RADs) (broken stick, log-series, power fraction, random fraction, Sugihara fraction, and two types of Zipf-Mandelbrot models) and resulting species-area relationships (SPARs) were studied (Fig. 1). It was shown that the model fit of the power function and the exponential SPAR model depends mainly on the number of species per unit of area, the fraction of singletons in the sample, and the total species number in the assemblage (Figs 2, 3, 4 and 5).

Sugihara and power fraction RADs did not necessarily lead to power function SPARs (Fig. 5) but are characterized by relatively high slope values in comparison to other distributions (Fig. 9).

Random placement and sampling of individuals did not lead to a proportional sampling for all distributions (Figs 6, 7, 8 and Table 1). Zipf-Mandelbrot and log-series distributions resulted in curvilinear local vs. regional plots (Fig. 6). The slope value  $z$  of the power function SPAR was not constant even for RADs with proportional sampling but depended on the total species number. The slope could be forced to become constant by introducing a correction factor into the po-

wer function SPAR. The implications of these findings for detecting local species saturation are discussed.

## 6. REFERENCES

- Amanieu M., Gonzalez P. L., Guelorget O. 1981 – Critères de choix d'un modèle de distribution d'abondances – *Acta Oec.* 2: 265–286.
- Aho J. M. 1990 – Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes (In: *Parasite Communities: Patterns and Processes*, Eds. G. W. Esch, A. O. Bush, J. M. Aho) – Princeton Univ. Press, pp. 157–196.
- Aho J. M., Bush A. O. 1993 – Community richness in parasites of some freshwater fishes from North America (In: *Species Diversity in Ecological Communities*, Eds. R. E. Ricklefs, D. Schluter) – Chicago Univ. Press, pp. 185–193.
- Bazzaz F. A. 1975 – Plant species diversity in old-field successional ecosystems in southern Illinois – *Ecology*, 56: 485–488.
- Caley M. J. 1997 – Local endemism and the relationship between local and regional diversity – *Oikos*, 79: 612–615.
- Caley M. J., Schluter D. 1997 – The relationship between local and regional diversity – *Ecology*, 78: 70–80.
- Colwell R. K., Coddington J. A. 1994 – Estimating terrestrial biodiversity through extrapolation – *Phil. Trans. R. Soc. Lond. B*: 345: 101–118.
- Connor E. F., McCoy E. D. 1979 – The statistics and biology of the species-area relationship – *Am. Nat.* 113: 791–833.
- Cornell H. V. 1985 – Local and regional richness of cynipine gall wasps on California oaks – *Ecology*, 66: 1247–1260
- Cornell H. V., Lawton J. H. 1992 – Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective – *J. Anim. Ecol.* 61: 1–12.
- Cresswell J. E., Vidal-Martinez V. M., Crichton N. J. 1995 – The investigation of saturation in species richness of communities: some comments on methodology – *Oikos*, 72: 301–304.
- Fisher A. G., Corbet S. A., Williams S. A. 1943 – The relation between the number of species and the number of individuals in a random sample of an animal population – *J. Anim. Ecol.* 12: 42–58.
- Frontier S. 1985 – Diversity and structure in aquatic ecosystems (In: *Oceanography and Marine Biology – An Annual Review*, Ed. M. Barnes) – Aberdeen, pp. 253–312.
- Gray J. S. 1987 – Species-abundance patterns (In: *Organization of communities – Past and Present*, Eds. J. H. R. Gee, P. S. Giller) – Oxford (Blackwell), pp. 53–67.



- Griffiths D. 1997 – Local and regional species richness in North American lacustrine fish – *J. Anim. Ecol.* 66: 49–56.
- Harte J., Kinzig A. P. 1997 – On the implications of species-area relationships for endemism, spatial turnover, and food web patterns – *Oikos*, 80: 417–427.
- Harte J., Kinzig, A. P., Green J. 1999 – Self-similarity in the distribution and abundance of species – *Science*, 284: 334–336.
- Hawkins B. A., Compton S. G. 1992 – African fig wasp communities: undersaturation and latitudinal gradients in species richness – *J. Anim. Ecol.* 61: 361–372.
- He F., Legendre P. 1996 – On species area relations – *Am. Nat.* 148: 719–737.
- Hubbell S. P. 1997 – A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs – *Coral Reefs* 16 Suppl.: 9–21.
- Hugueny B., Paugy D. 1995 – Unsaturated fish communities in African rivers – *Am. Nat.* 146: 162–169.
- Hugueny B., de Morais L. T., Merigoux S., de Merona B., Ponton D. 1997 – The relationship between local and regional species richness: comparing biotas with different evolutionary histories – *Oikos*, 80: 583–587.
- Kennedy C. R., Guégan J.-F. 1994 – Regional versus local helminth parasite richness in British freshwater fish: saturated or unsaturated parasite communities – *Parasitology*, 109: 175–185.
- Lawton J. H. 1990 – Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space – *Phil. Trans. R. Soc. Lond. B* 330: 283–291.
- Leitner W. A., Rosenzweig M. L. 1997 – Nested species-area curves and stochastic sampling: a new theory – *Oikos*, 79: 503–512.
- May R. M. 1975 – Patterns of species abundance and diversity (In: *Ecology and evolution of communities*, Eds. M. L. Cody, J. M. Diamond) – Belknap (Cambridge), pp. 81–120.
- Ney-Nifle M, Mangel M. 1999 – Species-area curves based on geographic range and occupancy – *J. Theor. Biol.* 196: 327–342.
- Pielou E. C. 1977 – *Mathematical Ecology* – John Wiley & Sons (New York).
- Preston F. W. 1962 – The canonical distribution of commonness and rarity. Part I and II – *Ecology*, 43: 185–215, 410–432.
- Rosenzweig M. L. 1995 – *Species diversity in space and time* – Cambridge, Univ. Press.
- Rosenzweig M. L. 1999 – Heeding the warning in biodiversity's basic law – *Science*, 284: 276–277.
- Srivastava D. E. 1999 – Using local-regional richness plots to test for species saturation: pitfalls and potentials – *J. Anim. Ecol.* 68: 1–16.
- Sugihara G. 1980 – Minimal community structure: an explanation of species abundance patterns – *Am. Nat.* 116: 770–787.
- Sugihara G. 1981 –  $S = CA^z$ ,  $z \approx 1/4$ ; a reply to Connor and McCoy – *Am. Nat.* 117: 790–793.
- Terborgh J. W., Faaborg J. 1980 – Saturation of bird communities in the West Indies – *Am. Nat.* 116: 178–195.
- Tokeshi M. 1990 – Niche apportionment or random assortment: species abundance patterns revisited – *J. Anim. Ecol.* 59: 1129–1146.
- Tokeshi M. 1993 – Species abundance patterns and community structure – *Adv. Ecol. Res.* 24: 111–186.
- Tokeshi M. 1996 – Power fraction: a new explanation of relative abundance patterns in species-rich assemblages – *Oikos*, 75: 543–550.
- Tonn W. M., Magnuson J. J., Rask M., Toivonen J. 1990 – Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes – *Am. Nat.* 136: 345–375.
- Ulrich W. 1999 – Estimating species numbers by extrapolation I: comparing the performance of various estimators using large model communities – *Pol. J. Ecol.*: 271–291.
- Ulrich W. 2000a – On species-area relationships I: Fit of power function and exponential model – *Pol. J. Ecol.* 48: 3–20.
- Ulrich W. 2000b – On species-area relationships III: The intercept of the power function and the exponential model – *Pol. J. Ecol.* 48: 37–48.
- Ulrich W. 2000c – On species-area relationships II: slope and factor values of power function and exponential model – *Pol. J. Ecol.* 48: 21–35.
- Westoby M. 1993 – Biodiversity in Australia compared with other continents (In: *Species Diversity in Ecological Communities*, Eds. R. E. Ricklefs, D. Schluter) – Chicago, Univ. Press, pp. 170–177.
- Williams M. R. 1995 – An extreme-value function model of the species incidence and species-area relations – *Ecology*, 76: 2607–2616.
- Wilson W. J. 1991 – Methods for fitting dominance/diversity curves – *J. Veg. Sci.* 2: 35–46.
- Wilson J. B., Gitay H., Steel J. B., King W. McG. 1998 – Relative abundance distributions in plant communities: effects of species richness and of spatial scale – *J. Veg. Sci.* 9: 213–220.
- Wissel Ch., Maier B. 1992 – A stochastic model for the species-area relationship – *J. Biogeogr.* 19: 355–362.