

Werner ULRICH

Nicholas Copernicus University in Toruń, Department of Animal Ecology  
Gagarina 9, 87-100 Toruń, Poland, e-mail: ulrich@cc.uni.torun.pl

## MODELS OF RELATIVE ABUNDANCE DISTRIBUTIONS I: MODEL FITTING BY STOCHASTIC MODELS

**ABSTRACT:** The present paper studies possibilities to discriminate between 9 stochastic models of relative abundance distributions (RADs). It develops a new test statistic for fitting based on least square distances and tests the applicability of methods described so far. The paper identifies three basic shapes of RADs termed power fraction, random assortment and Zipf-Mandelbrot type shape. It is shown that even a correct identification of the shape of a given data set requires that this data set is replicated more than 10 times. Estimates of necessary sample sizes for real animal or plant communities revealed that for communities with 20 to 100 species at least 200 to 500 times the species number is necessary for a correct model identification. The implications of these findings for the applicability of models of relative abundance distributions are discussed.

**KEY WORDS** relative abundance distribution, power fraction, random fraction, Sugihara fraction, Zipf-Mandelbrot distribution, model fit, least squares, confidence limits, sample size.

### 1. INTRODUCTION

Frequency or relative abundance distributions (RADs) have long been in the focus of ecologists either in the form of rank abundance plots or as measures of diversity and evenness. Early models focused on samples of species and tried to describe them by deterministic distribution orientated models like the geometric (Motomura 1932), the log-series (Fisher *et al.* 1943), the log-normal

(Preston 1948, 1962a ,b) and others. This situation began to change when May (1975) showed that the canonical log-normal is expected if an assemblage of species is influenced by many independent factors which act in a multiplicative way. Deviations from the canonical log-normal were therefore soon interpreted as resulting from disturbance factors (Patrick 1967, Gulliksen *et al.* 1980, Preston 1980, Ugland and Gray 1982, Frontier 1985) or pooled samples (Routledge 1980, Shaw *et al.* 1983, Hughes 1986). By allometric reasoning Harvey and Godfray (1987) argued that biomass or production data instead of densities will also not result in a "canonicity".

Critiques that all these models – being purely descriptions – lack ecological and evolutionary justification and their parameters being difficult to explain (Whittaker 1972, Pielou 1977, Routledge 1980), led Sugihara (1980, 1989) introducing his sequential breakage model, for which he showed that a sequential niche breakage process (with a fixed division probability of 0.75) leads to a log-normal type distribution which fits many natural (pooled) assemblages. Further support for his model came from the studies of Nee *et al.* (1991) and Gregory (1994) who showed that in species number – octave plots RADs of large natural assemblages (British birds) are not symmetrical (as predicted by a log-normal distribution) but – in accordance to the Sugihara model – left skewed. Recently, Tokeshi (1990, 1996) and Hubbell (1997) intro-



duced a whole set of new niche orientated (Tokeshi 1990, 1996) or species-turnover orientated (Hubbell 1997) models. Aim of all these renewed efforts was to interpret relative abundance distributions in terms of a few ecologically interpretable parameters and niche division processes.

However, despite a lot of recent theoretical (Tokeshi 1993, 1996, Bersier and Sugihara 1997) and empirical work (e. g.: Watkins and Wilson 1994, Wilson and Gitay 1995, Death and Winterbourn 1995, Hubbell 1997, Wilson *et al.* 1998, Peters and Bork 1999, Weiher and Keddy 1999) the study of relative abundance distributions has revealed less insight than had been hoped. On one side this is surely caused by a lack of understanding of density regulation and niche division.

But more important seems the confusion about which of the various models to be used and a general lack of connecting RADs with other methods to describe communities, especially measures of diversity and equitability (Lande 1996, Smith and Wilson 1996, Weiher and Keddy 1999, Wilson *et al.* 1999). It has also to be made clear whether the models should serve as pure descriptions of assemblages or samples (like diversity or evenness measures) as it was intended by the earliest researchers or whether they have to explain observed patterns. The first goal seems to be achievable. But it is not clear whether a best fit model will also be a model that describes ecological or evolutionary processes best. For the second goal much more empirical work has to be done to get large amounts of data sets to compare empirical RADs with environmental and historical data (Wilson *et al.* 1998).

A basic problem which has gained astonishingly few attention is how to fit various relative abundance distributions to empirical data and how to discriminate between models. (May 1975, Pielou 1977, Tokeshi 1990, Wilson 1991, Bersier and Sugihara 1997) and fitting was often done only by visual inspection (for example in the case of the large data set of Hughes 1986). Clear criteria for model fit are however necessary prerequisites for a correct model choice.

In the case of deterministic models least square techniques or non-parametric ones like the Kolmogorov-Smirnov tests have long been used (Eberhardt 1969, Pielou 1977, Wilson 1991, Bersier and Sugihara 1997) although they do not give clear

criteria for discrimination between models. In the case of stochastic models which do not produce fixed distributions Tokeshi favored the use of the 95% confidence limit of the model distribution as a test criterion: If more than 95% of the species of the empirical assemblage have relative densities inside the 95% confidence limit of the model distribution the model may be accepted as a fit. Bersier and Sugihara (1997) noticed some problems of this test mainly stemming from non-symmetric confidence limits at lower ranks and proposed a slightly different (but very time consuming) test statistic.

Despite the various proposed fitting procedures, up to now no comparative test of performance and discrimination power has been undertaken and existing reviews not or only briefly mention this theme (e. g. May 1975, Pielou 1977, Tokeshi 1993). For medium sized and larger communities it is not known whether it is in principle possible to discriminate between various models and how high sample sizes have to be to fit a model. However, for a model to be of scientific value, a least a theoretical possibility to discern it from others is necessary.

The first part of this study on relative abundance distributions tries therefore to solve some problems concerning model fit and discrimination between models. It concentrates on stochastic models because they have the realistic feature of possessing a variance. The second part (Ulrich 2001) will then relate the parameters of stochastic RADs to other measures of community structure such as evenness and diversity.

## 2. MATERIALS AND METHODS

### 2.1 MODELS TESTED

For the present paper 9 models of relative abundance distributions are compared: the Sugihara fraction (sequential breakage model); Sugihara 1980, Tokeshi 1996), the Mac Arthur fraction (the stochastic counterpart of the broken stick model; Tokeshi 1990), a stochastic version of the Zipf-Mandelbrot model (Frontier 1985) (see below), the random fraction and random assortment models (Tokeshi 1990), the overlapping niche, dominance decay, and particulate niche models (Tokeshi 1990), the power fraction model (Tokeshi 1996),



and the log-normal (Preston 1962a, b) (Fig. 1). The overlapping niche, dominance decay, and particulate niche models lead to even more equal distributions than the MacArthur fraction. The basic niche division processes gives Table 1. For detailed and lucid descriptions of the stochastic niche apportionment models and their basic properties see Sugihara (1980, 1989) and Tokeshi (1990, 1993, 1996).

Relative abundance distributions can be subsumed under three basic shapes (Fig. 2); firstly, a shape with a small number of very abundant and very rare species resulting in a S-shaped curve (in the following named power fraction type). This type of distribution

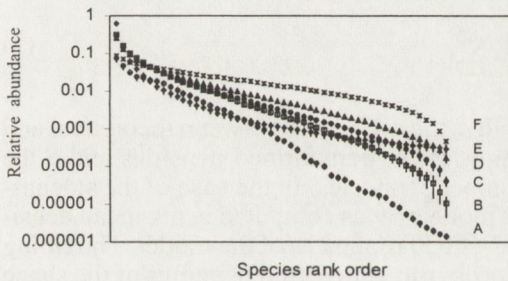


Fig. 1. Six models of relative abundance distributions (100 species each) in a semilogarithmic plot. A: random assortment ( $k = 0.3$ ), B: random fraction, C: Sugihara fraction ( $k = 0.75$ ), D: Sugihara fraction ( $k = 0.66$ ), E: Zipf-Mandelbrot ( $X = 0, k = 2$ ), F: MacArthur fraction. For the stochastic models means of 100 replicates each were taken. Given are also the 95% confidence limits after 100 replicates.  $X$  and  $k$  refer to the shape generating parameters of the models.

contains the classical log-normal, the overlapping niche, dominance decay and particulate niche models, the random fraction model, the broken stick model, the Sugihara fraction model, and the newly described model of Hubbell (1997); The second shape lacks the lower range of least abundant species (Zipf-Mandelbrot type distributions). Beside the Zipf-Mandelbrot model the dynamics model of Hughes (1984, 1986) and Tokeshi's (1990) composite model may also be subsumed under this type. A third shape also lacks the upper bound of very abundant species (random assortment type distributions). Here we find also the classical geometric series, the log-series, and the dominance preemption model. Fitting a theoretical distribution to an empirical data set may therefore be seen as a two step process: first establishing which of these basic shapes best applies and in a second step adjusting the parameter values. In the following both steps will be studied.

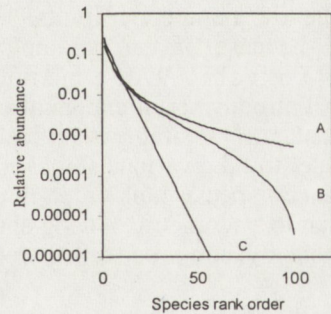


Fig. 2. Three basic shapes of relative abundance distributions. A: Zipf-Mandelbrot type, B: Power fraction type, C: Random assortment type.

Table 1. Sequential breakage models of relative abundance distributions and the way to choose the niche fraction and to divide this fraction during the sequential breakage process.  $ran$ ,  $ran_1$  and  $ran_2$  are linear random numbers in the range 0 to 1.  $S$  is the total number of species,  $x$  is the largeness of the niche fraction,  $i$  refers to the  $i$ -th species,  $X$  and  $k$  are the shape generating parameters of the models.

Model	Division probability distribution at	Select niche fraction at
Sugihara fraction	$k : 1-k \quad 0.5 \leq k < 1$	Random
Power fraction	Random	$ran x_i^k$ $-\infty < k < +\infty$
Random fraction	Random	Random
MacArthur fraction	Random	$ran x_i$
Random assortment	$ran^k \quad 0 < k \leq 1$	Always the smallest
Dominance preemption	Random	Always the smallest
Dominance decay	Random	Always the largest
Particulate niche	Random	None
Overlapping niche	$ran_1 - ran_2$	None
Stochastic Zipf-Mandelbrot	$1 / (ran + X)^k \quad 0 < k < \infty$	None



## 2.2. MODIFICATIONS OF SOME MODELS

The original sequential breakage model of Sugihara (1980) assumed a fixed division ratio  $k$  of 0.25:0.75 (in this paper  $k$  and  $X$  always refer to the division parameters of the models according to standard notation). However, other breakage ratios may be envisaged and they lead to different shapes of the model. For instance, a breakage ratio of 0.66 leads to a relative abundance distribution which is most similar to a canonical log-normal (Siegel and Sugihara 1983). This paper uses the model with ratios of 0.75 and 0.66. A normal division probability distribution around the envisaged division ratio was used similar to the original approach of Sugihara (1980) (who, based on some empirical data, favored a triangular division distribution, which is in fact a convenient approximation of normality). The variance of this normal distribution was adjusted to 0.085 and the distribution cut off at the lower and upper limits.

In the case of the random assortment model (Tokeshi 1990) a modification was used by introducing an exponent of the fraction constant. This simple modification allows the model to take various slopes in a log rel. abundance – species rank order plot (as in Fig. 1) similar to a geometric or a log-series model. This basic division process is therefore:

$$N_{i+1} = \text{rnd}^k \times N_i \quad (1)$$

with  $N_{i+1}$ ,  $N_i$  being the densities of species  $i$  and  $i+1$ ,  $\text{rnd}$  being a uniform random variable between 0 and 1 and  $k$  the shape producing constant ranging between 0 and 1. The slope in a log rel. abundance – species rank order plot (Fig. 1) has then a value of  $-k \log(2)$  at larger numbers of species and replicates. This makes it easy to fit this model from such plots.

To introduce a variance into the deterministic Zipf-Mandelbrot model which allows then better comparisons of the fit with other models the rank variable  $i$  was replaced by a random variable  $\text{rnd}$ , leading to

$$N_i = 1 / (X + \text{rnd})^k \quad (2)$$

with  $X$  and  $k$  the parameters of the model.

## 2.3. MODEL FITTING

The natural way to fit a theoretical distribution to a given data set is by least squares.

In the case of deterministic distributions this is the most often taken approach (Wilson 1991). In the case of stochastic models the method has not been applied due to the high variance in densities and their density dependence. Instead, Tokeshi's method using the 95% confidence limit of the model assemblages was preferred. However, this method proved to have only a low discrimination power (see below) which makes it desirable to look for an alternative. Additionally, it does not allow the estimation of parameter values. Therefore, in a first step a least square statistic was developed with a better discrimination power.

The main fitting variable  $r$  of the least square method was:

$$r = \sum_{i=1}^S (d_i)^2 \quad (3)$$

with  $d_i$  the difference between theoretical and empirical ln-transformed densities and  $S$  the number of species. In the case of the stochastic models  $r$  was computed using mean densities of 100 replicates of the model. The fitting process run with different values of the shape generating parameters  $k$  and  $X$  (by stepwise enclosure) until  $r$  reached a minimum.

This test value is sensitive to the maximum density difference  $D$  of the species – defined as the quotient of most and least abundant species – of the data set (Fig. 3) (in this paper data set always refers to an assemblage to be fitted). In the stochastic models low density species effect the value of  $r$  overproportional, mainly due to the higher variance. This makes it difficult to compare fits by different models.

Additionally, due to the summation process the test statistic  $r$  will depend on the total number of species  $S$  when comparing fits from assemblages of different species numbers. At first sight, the quotient  $r/S$  should be constant. However, the higher the number of species the lower the total variance after a finite number of iterations (100 in the present cases). Therefore  $r$  will be lower at high species numbers. To use  $r$  as a test statistic for comparing the fits of stochastic models at least a correction factor for density is necessary. If one wants to compare  $r$  at different species numbers a second correction factor has to be added.

Figs 3 A to C show the dependence of  $r$  on the max. density difference in the data set and Figs 3 D to F give the dependence of the



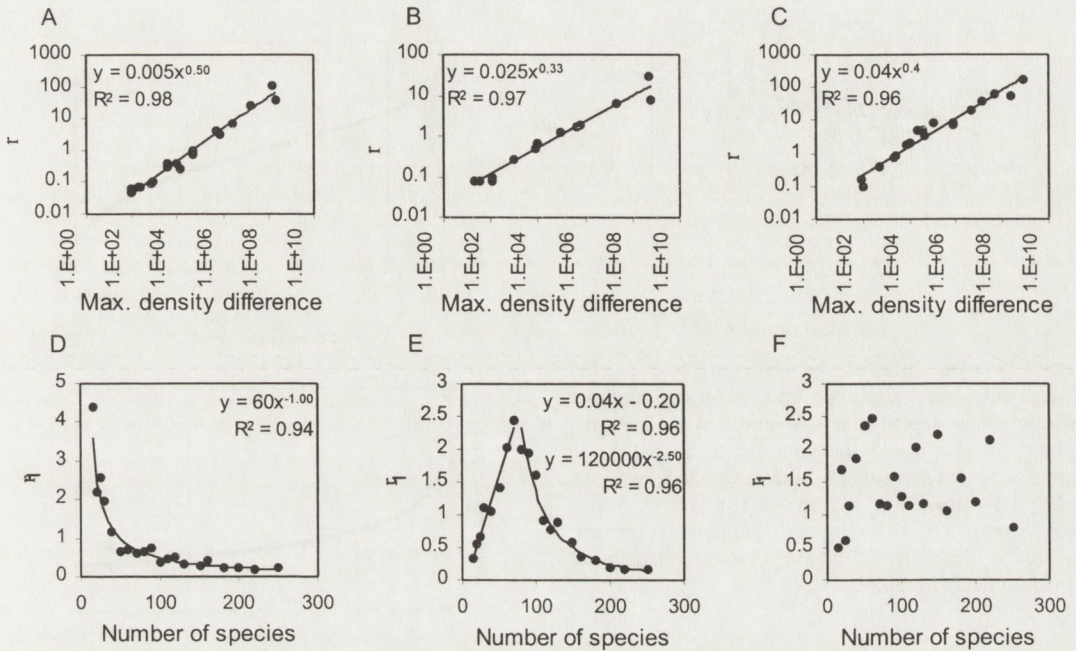


Fig. 3. Dependence of the least square test statistics  $r$  (equation 3, termed  $r_l$  after correction for dependence of the maximum density difference) on the maximum density difference (A to C) in the data set and the number of species (D to F). Results of 20 power fraction (A:  $k = -2$  to  $2$ , 50 species each; D:  $k = 0.1$ ), random assortment (B:  $k = 0.05$  to  $0.8$ , 50 species each; D:  $k = 0.2$ ), and stochastic Zipf-Mandelbrot data sets (C:  $k = 1$  to  $8$ ,  $X = 0$ , 50 species each; F:  $k = 2$ ,  $X = 0$ ). The assemblages were computed (means of 100 replicates) and then fitted by the same model. The data points are mean values of 100 fitting procedures each.  $R^2$ : variance explanation of the regression given. Symbols as in Fig. 1.

density corrected  $r$  (denoted as  $r_l$ ) on species number for all three types of model shapes.

Introducing the equations given in Fig. 3. (as correction factors) into equation (3) and rearranging conveniently results in the following least square test statistic for stochastic relative abundance distributions:

1. Random assortment type distributions:

$$r_{test} = 1000 \frac{r}{(S-5) \times D^{1/3}} \quad 5 < S \leq 70 \quad (4)$$

$$r_{test} = \frac{1}{3000} \frac{r}{S^{-2.5} \times D^{1/3}} \quad S > 70 \quad (5)$$

2. Power fraction type distributions

$$r_{test} = \frac{1}{3} \frac{r}{S \times D^{1/2}} \quad (6)$$

3. Zipf-Mandelbrot type distributions

$$r_{test} = 25 \frac{r}{D^{2/5}} \quad (7)$$

Of course, the value and the variance of  $r_{test}$  depends highly on the number of replicates in the data sets but it appeared that the variance dependence of  $r_{test}$  is the same for all three types of distributions and that above 50 replicates  $r_{test}$  becomes constant (data not shown). Good fits are then in every case characterized by values of  $r_{test}$  near or below 1 (Fig. 4). Values above 10 can hardly be called fits.

Fig. 4 shows a performance test of  $r_{test}$  for all three types of distributions. The test was done by computing 100 replicates each of a Sugihara fraction, a random assortment and a Zipf-Mandelbrot distribution and afterwards fitting these data sets by the same models. For species numbers between 20 and 250 and accompanying density differences between  $10$  and  $10^8$   $r_{test}$  was roughly constant ranging between 0.03 and 3.3 (power fraction), 0.14 and 4.3 (random assortment), and 0.73 and 4.4 (stochastic Zipf-Mandelbrot). All data points lie inside the range of 2 standard deviations of each model (data not shown).



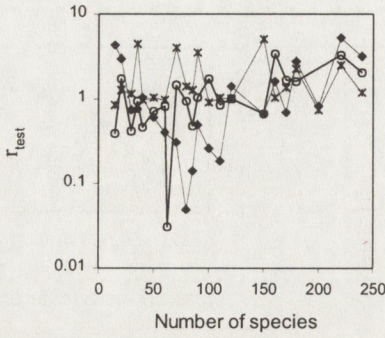


Fig. 4. Performance of the test statistic  $r_{test}$  after corrections for density and species number differences in dependence (Equations 4 to 7) on the number of species in the data set to be fitted. 20 data sets were each fitted by the same model and the data points are mean  $r_{test}$  values (of 100 replicates each) for each fit. Circles: random assortment, squares: Sugihara fraction, stars: stochastic Zipf-Mandelbrot model.

The above results make it possible to develop a test statistic to discriminate between stochastic models. After fitting the data set several times (conveniently more than 100 times) by the model distributions the 95% confidence limit of the resulting  $r_{test}$  values has to be computed according to:

$$CF = 1.96\sigma / \sqrt{n} \tag{8}$$

with  $CF$  being the confidence limit,  $\sigma$  the standard deviation of the  $r_{test}$  values, and  $n$  the number of fitting processes. A model (*model1*) is accepted to fit better than another (*model2*) if 95% of the  $r_{test}$  values are below the 95% confidence limit of the other model. A test statistic can therefore be defined as

$$Q_{ls} = \frac{\text{Number}\{r_{test}(\text{model1}) > CF[r_{test}(\text{model2})]\}}{n} \tag{9}$$

with  $CF(r_{test}(\text{model2}))$  being the lower 95% confidence limit of *model2*. Acceptance occurs at  $Q_{ls} < 0.05$ .

The most easiest way to discriminate between the shapes given in Fig. 2 is to determine whether more species of the upper or the lower 15-percentile have densities above (Zipf-Mandelbrot) or above and below (power fraction type) the straight line defined by the middle ranking species than expected by chance (Fig. 5). If this probability is less than 0.95 no clear deviation from the random assortment type is stated. The test is applicable if a data set contains more than 15 species.

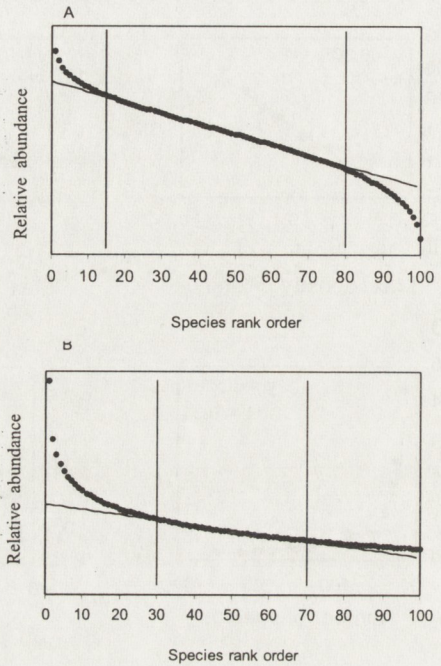


Fig. 5. Shapes of a Sugihara fraction (A) and a Zipf-Mandelbrot model (B). Given are in both cases regressions through the middle ranking species (excluding the upper and lower 30% of species). Given are also the points (indicated by the vertical lines) above and below which the relative abundances are above or below this regression.

### 3. RESULTS

#### 3.1. DISCRIMINATION BETWEEN TYPES OF MODELS

In a first step it was established how many replicates of the data sets are necessary to identify the type of distribution (power fraction, random assortment or Zipf-Mandelbrot type). For Fig. 6 2800 data sets (20 to 100 species) each of a Sugihara fraction ( $k = 0.75$ ) and a stochastic Zipf-Mandelbrot distribution ( $k = 2, X = 0$ ) were computed, 100 times each as a mean of 3, 5 and 10 replicates and 100 times each without replication (a single data set). This can be compared by taking natural communities from a single observation or from 3, 5 and 10 replicated observations. Preliminary tests showed that for data sets containing less than 20 species extraordinary high numbers of



replicates (in most cases more than 50) are necessary to discriminate even between the types of models. It is therefore probably of little value to fit RADs to such small natural communities.

Fig. 6 and Tables 2, 3 show that the possibility to discriminate a power fraction or a Zipf-Mandelbrot type model from a random assortment model depends on the number of species and the number of replicates of the data sets. For non-replicated data sets it proved to be impossible to distinguish between these three models at a 5% error level

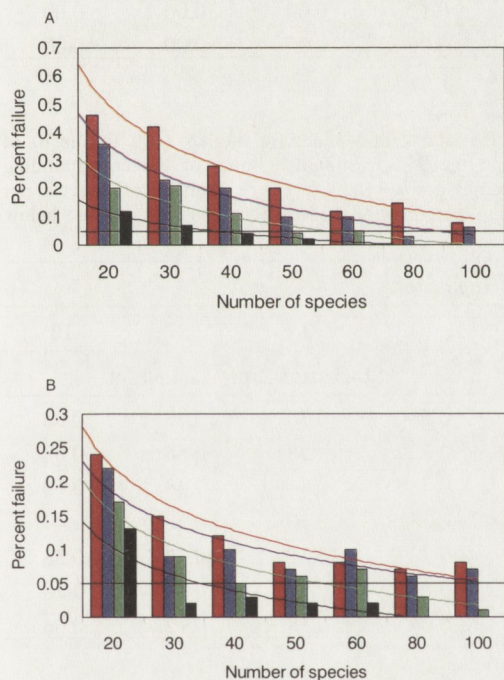


Fig. 6. Percentile test (Fig. 5) to discern between type A, B, or C assemblages in Fig. 2. A: Discrimination between random assortment and power fraction type models: fraction of assemblages (of a total of 100) of Sugihara fraction assemblages ( $k = 0.75$ ) which failed to pass the test (i. e. which have less than 95% of their upper and lower 15% species above or below the regression through their inner 40 species). B: the same test to discriminate between Zipf-Mandelbrot and power fraction type: same assemblages (given is the fraction of assemblages which have less than 95% of their upper and lower 15% species above the regression through their inner 40 species). Given are also logarithmic regressions for each number of replicate. Bars and regression line in red: single data set, in blue: data set is a mean of 3 replicates, in green: data set is a mean of 5 replicates, in black: data set is a mean of 10 replicates. The horizontal line shows the 5% error level.

even if the data set contained 100 species (Figs 1 and 6, Tables 2, 3).

To discriminate between a power fraction and a random assortment type (Fig. 6A) or a Zipf-Mandelbrot and a power fraction type model (Fig. 6B) 10 replicates were necessary and the data set had to contain at least 30 species. If the data sets contained more than 50 species 5 replicates proved to be enough. The least square  $Q_{ls}$ -statistic (equation 9) gave in the first case nearly identical results but performed better when discriminating between the random assortment and the Zipf-Mandelbrot type models (Table 2). In this case 3 replicates proved to be enough for species numbers above 50.

The least discrimination power has the Tokeshi method using the 95% confidence limit of species densities (Table 3). Even with 10 replicates of the data set and 100 species it was not possible to discriminate between a random assortment and a power fraction type model at a 5% error level.

### 3.2. DISCRIMINATING BETWEEN MODELS OF THE SAME TYPE

The Zipf-Mandelbrot type distributions (this, their stochastic counterpart, and the dynamics and the composite models) depend all on two or three shaping parameters which makes a correct model identification nearly impossible. All so far proposed random assortment type distributions (the geometric, the log-series, and dominance preemption, and the random assortment) have exactly the same shape which makes it also impossible to discriminate between them. These distributions may be used alternatively as pure descriptions but not as explanations for the observed pattern.

In the case of the power fraction type several models have been proposed with slightly different properties and shapes. The power fraction, Sugihara fraction, the Hubbel model, and the log-normal model all contain more than one shape generating parameter (at least  $S$  and  $k$ ) which allows a tuning of shape. This makes it very difficult to discriminate between them in real data sets. The deterministic log-normal is point symmetrical (in log abundance – species rank order plots) whereas most other models have more rare than abundant species. This results in species number – octave plots with a left skewed shape (Fig. 7). By examining the skewness of the distribution and using very large data sets



Table 2. Least square test statistic  $Q_{ls}$  comparing fits of the data set (a Sugihara fraction) by the same Sugihara fraction assemblages with fits by a random assortment and the stochastic Zipf-Mandelbrot model.  $S$ : number of species. Correct model identification needs values below 0.05. For each data point 100 replicates of each model were computed

S	Data set replicates							
	1	3	5	10	1	3	5	10
	Random assortment				Stochastic Zipf-Mandelbrot			
20	0.92	0.90	0.88	0.78	0.92	0.38	0.38	0.02
30	0.88	0.70	0.50	0.14	0.76	0.16	0.00	0.00
40	0.76	0.50	0.18	0.04	0.34	0.22	0.00	0.00
50	0.72	0.30	0.10	0.00	0.36	0.00	0.00	0.00
60	0.58	0.10	0.06	0.00	0.28	0.00	0.00	0.00
80	0.36	0.02	0.00	0.00	0.12	0.00	0.00	0.00
100	0.34	0.02	0.00	0.00	0.06	0.00	0.00	0.00

Table 3. Fraction of fits by the random assortment and the stochastic Zipf-Mandelbrot models (100 fits each) of which more than 5% of species had relative abundances inside the 95% confidence limits of the corresponding species of the data set (Sugihara fraction) being fitted. Assemblages as in Tab. 1.  $S$ : number of species per assemblage. For each data point 100 replicates were computed. A correct model identification needs a value below 0.05.

S	Data set replicates							
	1	3	5	10	1	3	5	10
	Random assortment				Stochastic Zipf-Mandelbrot			
20	0.90	1.00	1.00	1.00	0.68	0.70	0.78	0.88
30	0.80	0.96	0.98	1.00	0.22	0.58	0.66	0.68
40	0.80	0.96	1.00	1.00	0.38	0.44	0.48	0.60
50	0.80	0.98	1.00	1.00	0.38	0.30	0.38	0.44
60	0.80	0.98	0.98	1.00	0.38	0.36	0.28	0.38
80	0.82	0.94	0.96	0.96	0.06	0.20	0.14	0.28
100	0.82	0.90	0.84	0.76	0.06	0.18	0.12	0.06

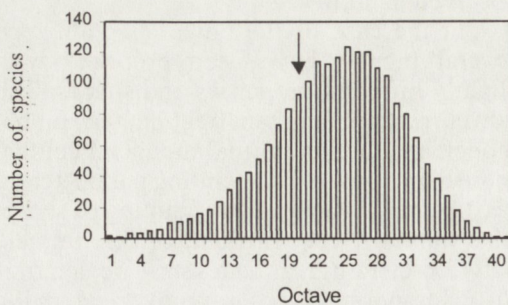


Fig. 7. Frequency (number of species) – octave ( $\log_2$  abundance class) plot of an assemblage with 2000 species distributed according to a random fraction model (Model B in Fig. 1). The distribution is not symmetrical but left skewed. The arrow indicates the modal octave.

it is possible to identify these distributions. This had been undertaken by Nee *et al.* (1991) and Gregory (1994) who showed that real large heterogeneous assemblages (British birds) are indeed skewed therefore rejecting the log-normal model.

The other power fraction type distributions depend only on species number although it is easy to introduce additional parameters that allow a tuning of shape (see for instance Büssenschütt and Pahl Wostl (1999) in the case of the broken stick distribution) and model discrimination is in principle possible by an ordinary fitting process. Table 4 gives the relations between the models and shows that all of them can be replaced by a power fraction (or by a log-normal).



Tab. 4: Relations between models of the power fraction type. Fraction parameter  $k$  of the power and the Sugihara fraction that lead to the same shapes than other models.

Fixed models	Power fraction	Sugihara fraction
Canonical log-normal	0.07	0.66
MacArthur fraction	1	–
Dominance decay	10	–
Overlapping niche	1.9	–
Random fraction	0	0.81
Particulate niche	40	–

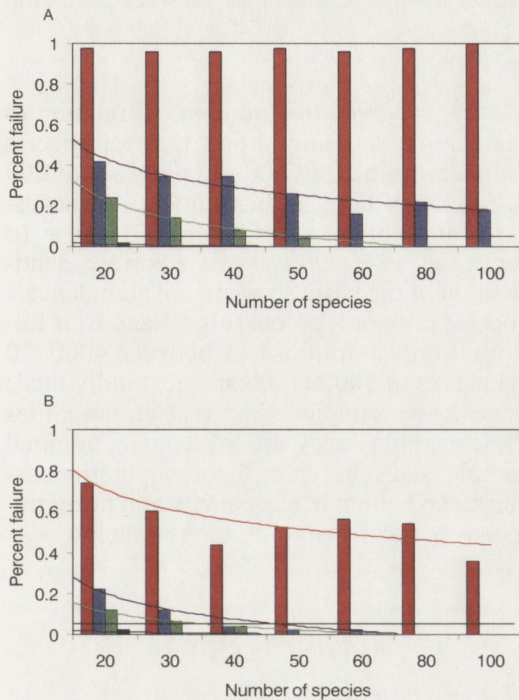


Fig. 8. Possibility to discriminate between random fraction and Sugihara fraction ( $k = 0.75$ ) models of relative abundance distributions. A: Tokeshi's 95% confidence limit criterion. B:  $Q_{ls}$  statistic (equation 8). The shapes of the assemblages are given in Fig. 1. Given are also logarithmic regressions for each number of replicate. Bars and regression line in red: single data set, in blue: both data sets are means of 10 replicates, in green: both data sets are means of 20 replicates, in black: both data sets are means of 30 replicates. The fractions inside the 95% confidence limit refer to the number of comparisons (from a total of 100 replicates) which do not pass these tests. The horizontal line shows the 5% error level.

How many replicates of the data set are necessary for a correct identification of one of these models? With the exception of the MacArthur fraction (which is identical with a power fraction with shaping parameter  $k = 1.0$ ) correct identification of the models given in Table 4 requires more than 100 replicates of the data set (data not shown).

For other models Fig. 8 shows again that discrimination ability depends on the number of replicates and the species number of the data sets. For species numbers above 50 data sets have to be replicated at least 10 times to discriminate between a random fraction and a Sugihara fraction assemblage (with  $k = 0.75$ ). Again the above defined  $Q_{ls}$  statistic performed better than the 95% confidence limit criterion of Tokeshi. The latter method required at least 30 replicates to discriminate between models in assemblages of only 20 species. Assemblages having fewer than 20 species will require extraordinary high numbers of replicates for a correct model identification.

A similar test as in Fig. 8 was performed using Sugihara fractions with  $k = 0.75$  and 0.66 and a MacArthur fraction (for shapes see Fig. 1). A discrimination between both Sugihara fraction models required with both above used methods 10 replicates. For a discrimination between the Sugihara and the MacArthur fraction single data sets are enough (data not shown).

### 3.3. ESTIMATING NECESSARY SAMPLE SIZES

Transferring the above results to real data sets requires that species of real communities have the same variability than the model species and the necessary number of replicates depends not only on species numbers but also on the number of individuals per sample. Natural density variability in comparison to model variability has up to now not been studied and for simplicity we have to assume similar variability. Under this assumption the sample size can be estimated.

Of course, the upper sample size is to sample the whole community like in the bird studies of Nee *et al.* (1991) and Gregory (1994). In this case the necessary sample size is the quotient of the relative densities of the least and the most abundant species. In real samples this can be approximated by the multiplication of the density of the most abundant species with the total area studied.



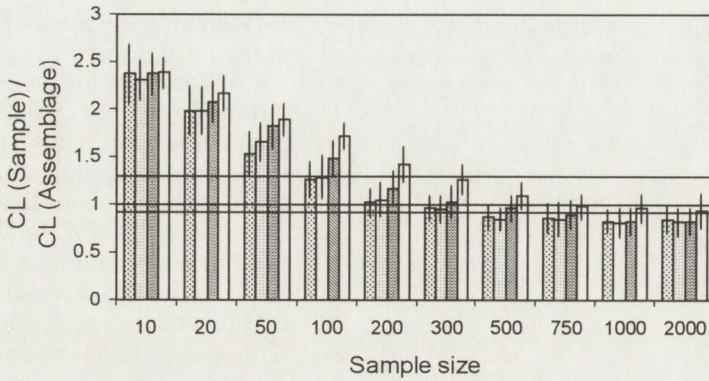


Fig. 9. Estimating the necessary sample size for model discrimination (given as multiple of species number) by comparison of the confidence limits of  $r_{test}$  ( $CL$ ) of samples (10 replicates) with that of the whole assemblage (Sugihara fraction with  $k = 0.75$ , 5 replicates) at different species numbers. The horizontal lines indicate the sample sizes below which the sample confidence limit is less than that of the assemblage (0.94 at 9 replicates, 1 at 5 replicates, and 1.31 at 3 replicates of the assemblage). Given are also standard deviations of the test statistic after 100 replicates. First bar of each sample size: 20 species per assemblage, second bar: 30 species, third bar: 50 species, fourth bars: 100 species.

However, this method leads at higher species numbers to astronomically high sample sizes. For instance a Sugihara fraction assemblage of 200 species would require more than 1500000 individuals to be sampled. In reality, much lower sample sizes are necessary for a correct model identification. This sample size may be estimated by comparing the variances of  $r_{test}$  of samples with different numbers of replicates.

Figs 6 and 8 and Tables 2 and 3 showed that in many cases 10 replicates would be enough for model and especially model type discrimination but that lower numbers are too low. That means the variance of  $r_{test}$  at 10 replicates (and using the whole community) is small enough. We can now compute how many individuals a sample of 10 replicates has to contain that the variance of  $r_{test}$  is less than that of the whole community at say 5 or 9 replicates. This was done by computing 4000 Sugihara fraction assemblages ( $k=0.75$ ) with 20, 30, 50, and 100 species. From 100 assemblages of each species number and each sample size 10 random samples each were taken. The number of individuals per sample (the sample size) was 1 to 200 times the number of species leading to a total sample size of 10 to 2000 times the species number (Fig. 9). Next, the variance of  $r_{test}$  at each sample size and species number and the according variance of the whole community after 3, 5 and 9 replicates was determined. The sample size is large enough if the quotient of the accompanying confidence limit (equation 8) of both is less than 1.

Fig. 9 gives this quotient in relation to the sample size and shows that for species numbers from 20 to 100 sample sizes of 200 to 500 times these species numbers are necessary for a correct identification. Because 10 replicates were necessary for a correct identification of the basic shape in log abundance – species rank order plots (Figs 2 and 6) it follows that even for this task between 4000 (20 species) and 50000 (100 species) individuals have to be sampled. For real communities these sample sizes are of course minimal sample sizes because the computation assumes no habitat heterogeneity and no aggregated spatial distribution of the species.

#### 4. DISCUSSION

The problem of how to fit models of relative abundance distributions to ecological data has gained much less interest than developing models. Pielou's (1975) statement that little or no work has been done on the applicability of certain models to data from single, natural communities still holds even after 25 years. Most "fits" in older work appear to be simple comparisons of curves and data points by eye (Wilson 1991) and Wilson's *et al.* (1998) conclusion that many older statements on relative abundance distributions have only few or no foundations and had never been tested seriously is surely correct.



The most straightforward attempt to solve the problem of fitting stochastic models was the proposition of Tokeshi (1990, 1993) to use the 95% confidence limit of densities as a test criterion. Additionally, the distribution of species ranging outside this limit has to be studied. If the 5% outliers are not randomly distributed the fit has also to be rejected. However, the present test of the method shows that its discrimination power is low, a fact which greatly limits the applicability of the test.

In general, the present results are not promising. Despite the large and confusing number of models proposed so far (including the deterministic models not dealt with in this paper more than 15) it seems that nearly all of them are of few scientific value because they do not contain the possibility for testing them under realistic conditions. This is especially true for models which depend on more than one shaping parameter (the species number). The identification of three basic shapes of models may therefore be a step forward. They can be described by three generating models, for example a random assortment, a power fraction, and a Zipf-Mandelbrot model and a next step in studying RADs may be to establish whether, how often and where these three shapes occur in nature.

The evidence for the existence of Zipf-Mandelbrot shapes is quite weak (Frontier 1985, Hughes 1986, Ulrich 2000), and the notion that random assortment type distributions are found in small communities or at early stages of succession has never been tested seriously (Wilson *et al.* 1998). It may be that in reality only various types of power fraction type distributions occur and that evidences for other types stem from small samples or non-replicated data sets which do not allow a correct identification of shape (Weiher and Keddy 1999). The standard textbook references for geometric type distributions at early stages of succession (Whittaker 1972, Bazzaz 1975) for instance are well fitted by log-normal or Sugihara fraction distributions (Kempton and Taylor 1976, Ulrich unpubl.). In this respect, the findings of ecosystem modelers deserve attention. Ebenhöh (1988) and Büssenschütt and Pahl-Wostl (1999) found in model ecosystems that large late succession communities always tend to be more equally distributed than predicted by conventional theory which assumes a Sugihara fraction (May 1975, Sugihara 1980, Nee *et al.* 1991, Toke-

shi 1996). It may be that communities rather start from a Sugihara fraction distribution and end in a situation where all species have similar density ranges, that is where they follow a Poisson (or particulate niche) distribution.

The present paper also gives estimates for sample sizes to discriminate between types of models. These sample sizes are quite high and throw further doubt on older empirical work on RADs. Samples sizes of 200 to 500 times the species numbers are only rarely reached and it should be noted that these sample sizes are minimum values assuming random distributions of species without taking aggregation or habitat heterogeneity into account. These factors (among others) would lead to even higher sample sizes. Much work has been done with single data sets (see for instance the large compilation of Hughes 1986) of unknown variance of species density and of density fluctuations. These papers cannot be taken as unequivocal evidence for random assortment types of RADs in small or early successional stage communities.

Of course, all the estimates presented here assume a natural density-variability which is similar to the variability of the model distributions (which is also not constant throughout the models). Unfortunately, I am not aware of any study comparing natural variability with model predictions. Additionally, the study of variability patterns is still at the beginning. Pimm's (1993) claim that he knows of only two such studies (Pimm 1991, Schoener and Spiller 1992) still holds and his list has to be added by only a few newer papers (Vandermeer 1993, Kunin and Gaston 1997, Ferriere and Cazelles 1999). These few studies point to a left skewed density probability distribution in real communities with a preponderance of low and intermittent density stages. The preliminary work of Bersier and Sugihara (1997) on the MacArthur fraction model shows in this distribution rather the opposite skewness. Clearly, a lot of empirical work has to be done to fit theoretical distributions not only using means but also by comparisons of variability patterns.

ACKNOWLEDGMENTS: I thank Prof. J. Buszko and Dr. Kartanas for critical and valuable suggestions on the manuscript. The suggestions of an anonymous reviewer improved the methods section. Miss H. Pearson kindly improved my English.



## 5. SUMMARY

The present paper studies possibilities to discriminate between 9 models of stochastic relative abundance distributions (RADs) (Figs 1, 2, 5, 6, Tables 1, 4), develops a new test statistic for fitting based on least square distances (Figs 3 and 4) and tests the applicability of methods described so far. The paper identifies three basic shapes of RADs termed power fraction, random assortment and Zipf-Mandelbrot type shape (Fig. 2). It is shown that even a correct identification of the shape of a given data set requires that this data set is replicated more than 10 times (Figs 7, 8, Tables 2, 3). Estimations of necessary sample sizes for real animal or plant communities showed that for communities with 20 to 100 species at least 200 to 500 times the species number is necessary for a correct model identification. The implications of these findings for the applicability of models of relative abundance distributions are discussed.

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(Received after revising August 2000)