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RELATIVE ABUNDANCE DISTRIBUTIONS OF SPECIES: THE NEED TO HAVE A NEW LOOK AT THEM

ABSTRACT: This paper shows that recent models of relative abundances (RADs) like the log--normal model or sequential breakage or niche apportionment models are not able to describe and explain RADs found in natural communities because they are derived from a classical niche concept and assume strong past or present interspecific competition. None of them refers especially to temporal variability and functional niche dimensions. The present paper identifies three basic features of natural communities (unimodal species–weight distributions, abundance–weight distributions with more or less marked upper boundaries, and species density fluctuations that can be modelled by four different random processes). Modelling communities with these basic features resulted in RADs that only in part could be described by classical models but that had shapes often found in samplings from larger natural communities. No single distribution like the canonical log-normal appeared that may serve as a general null-model but RAD and evolutionary strategy (r- or K selection) seem to be related. The shape of relative abundance distributions was found to depend on the number of species even if all parameter setting of the generating distributions were identical. This indicates that classical evenness indices (that assume independence of species number) might not be appropriate to compare communities with different numbers of species. It appeared that RAD and body weight related community patterns have to be studied together.

KEY WORDS Relative abundance distribution, RAD, sequential breakage, abundance–weight distribution, species – weight distribution, temporal variability, niche, evenness

1. INTRODUCTION

The question what factors cause abundance differences between species in a community has intrigued ecologists from the beginning of the century. Classical competition theory pointed to different resource use and to niche differentiation during ecological and evolutionary time together with pronounced levels of interspecific competition (see reviews by Walter 1988, Griesemer 1992, Colwell 1992). On this basis a plethora of models has been developed aimed to describe or even to explain abundance differences and relative abundance distributions (RADs) in real plant or animal communities. Most noticeable among the older models are Motomura's geometric series (Motomura 1932), the log-series of Fisher et al. (1943), MacArthur's (1957) broken stick distribution and especially Preston's (1962) canonical log-normal distribution. In these models species relative abundances are assumed to be describable by certain statistical distributions.

However, they have long been criticised of lacking deeper ecological foundation and that their parameter values are difficult to ex-

plain in ecological terms (Tokeshi 1990, 1993). But to a certain extent this critique fells short. Especially the log-normal was not designed to explain RADs but to describe them and to give a convenient summary statistic of community structure. In this sense the log-normal was used by Kempton and Taylor (1976) to develop a diversity statistic. However, the work of Sugihara (1980) Nee *et al.* (1991) and Gregory (1994) showed that the log-normal model is not the good descriptor of community structure as has been thought. The log-normal predicts equal numbers of very abundant and very rare species. From the study of relative abundances of British birds however it appeared that real large communities are unsymmetrical in having more very rare species (Nee *et al.* 1991, Gregory 1994).

Today, stochastic niche apportionment models (Sugihara 1980, 1989, Tokeshi 1990, 1993, 1996, Mouillot *et al.* 2000, Ulrich 2001a) that base on a sequential breakage process are more popular. They indeed predict unsymmetrical shapes in abundance –

species rank order plots and they allow – to a certain extent – to include natural variation in abundance.

All of these models, even a recently published one based on fractal geometry (Mouilliot *et al.* 2000, but see Bell 2000), rely on a classical concept of niche and niche division. A fixed amount of a limiting resource is assumed of being divided among the species. A two step division process that is visualised in Fig. 1 may describe nearly all of the current models. A total niche space is first broken into two parts at a given probability distribution. One of the parts is then chosen at a part-size dependent selection probability for further breaking. Table 1 contains the most important models of relative abundance distributions and shows their breakage algorithms. Silently, these models also assume strong (present or past) interspecific competition as factors to stabilise abundances inside certain ranges. This is necessary to overcome the problem of large stochastic variability in time.
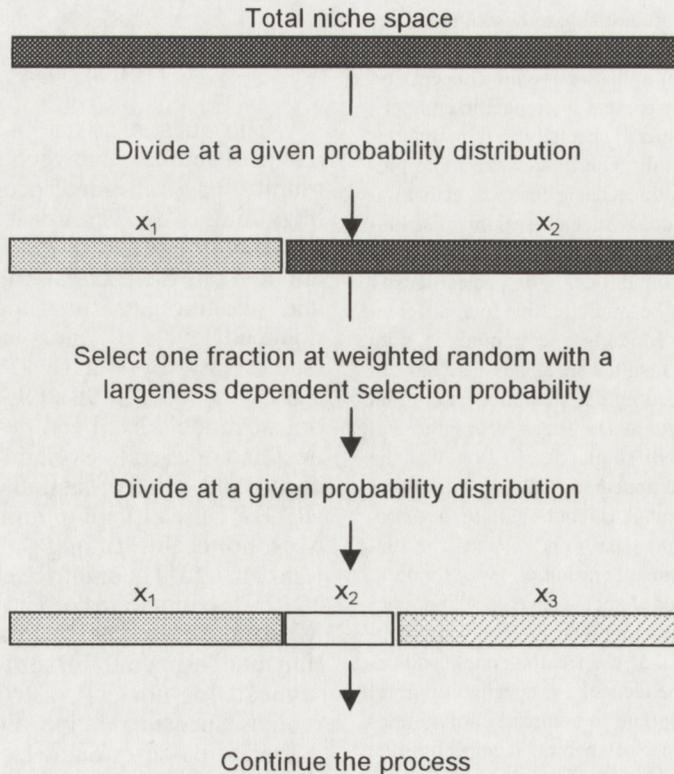

Fig. 1. The sequential breakage process generating relative abundance distributions starts from an unbroken total niche space, divides this with a given probability distribution, and then selects with a weighted probability one of the fractions x. The process continues until the number of fractions reaches the envisaged species number. Figure modified from Tokeshi (1996).

Table 1. Stochastic 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. Given are also equivalent deterministic models

Stochastic Model	Equivalent deterministic model	Division probablity distribution at	Select niche fraction at
Sugihara fraction	Log-normal	$k : 1-k$ $0.5 < k < 1$	Random
Power fraction	Log-normal	Random	$ranx_i^k$ $-\infty < k < +\infty$
Random fraction		Random	Random
MacArthur fraction	Broken stick	Random	$ranx_i$
Random assortment	Geometric series, log-series	ran^k $0 < k < +\infty$	Always the smallest
Dominance preemption	Geometric series, log-series	Random	Always the smallest
Dominace decay		Random	Always the largest
Particulate niche		Random	None
Overlapping niche		$ran_1 - ran_2$	None
Fractal model	Zipf-Mandelbrot	Accumulation of whole branching trees at certain probability distributions	
Stochastic Zipf-Mandelbrot	Zipf-Mandelbrot	$1 / (ran+X)^k$ $0 < k < \infty$	None

However, the classical niche concept of Hutchinson (1957, 1959) and MacArthur (1967) and MacArthur and Levins (1967) underwent recently major refinements and a general redefinition (Leibold 1995, 1998, Wiesheu 1998, Austin 1999). In modern niche theory species may coexist if there is a trade off in the requirements of the species and if there are species-specific effects of the factor that most limits its growth (Leibold 1995). This means that species may coexist not only if they are sufficiently separated by classical niche dimensions (morphological, temporal, resources or habitats) but also in functional ones like dispersal ability, aggregation, growth-rate or temporal variation in abundance. Additionally, competition was found to be of considerably less importance than has been assumed by earlier theory (Connell 1980, Shorrocks et al. 1984). Any analysis of niche segregation has therefore to embrace classical and functional niche dimensions. Nearly all models of relative abundance distribution (an exception is Hughes' (1984, 1986) seldom used dynamics model) only refer to classical resource orientated niche dimensions.

The notion that spatial and temporal variability as well as resource distributions that lead to non-equilibrium conditions allow much more species to coexist than predicted by classical niche theory (Gurney and Nisbet 1978, Shorrocks et al. 1979, 1984, Shorrocks and Rosewell 1987, Sevenster 1996) contradicts the basic reasoning of most of the niche apportioning models. The recent finding of Huisman and Weissing (1999) is in this respect of special interest. These authors found that in classical Lotka – Volterra competition models coexistence of a large number of species is permitted despite limited resources simply due to the dynamic properties of these models. They showed that more than two limiting resources result in chaotic variation of species density. These density fluctuations then itself allow much more species to coexist than predicted by the classical principal of competitive exclusion. The species of these models show relative abundance distributions (in this paper density and abundance of model species are treated as being synonymous) that may be described by one or another of the existing models, but

in neither case are the theoretical foundations of these models (niche divisions) applicable.

Additionally, in non-equilibrium communities or in the ones that are driven by the dynamic properties of the system we will often be confronted with a situation that at each time (each year or each generation) another model of relative abundance will best apply. This problem has long been known (Preston 1948, Pielou 1977, Tokeshi 1993) and raises genuine questions about the way of model choice. But it has been merely treated as a statistical artefact (Preston 1948, Pielou 1977, Bersier and Sugihara 1997) that has to be overcome by taking larger sample sizes or longer time series. However, for real communities this will be impossible in most cases. In an earlier paper I showed (Ulrich 2001a) that even to achieve a minimal discrimination power sample sizes have to be 200 to 500 times the number of species. For communities with more than 20 species stable results are obtained only above 30 replicates (sampling years or generations). For smaller communities even more replicates have to be taken. Such high sample sizes are for natural communities nearly impossible to be obtained making the application of classical stochastic models of relative abundance a dubious task. Additionally, community structure and relative abundances of species may change continuously over time as has recently been shown by Bengtsson *et al.* (1997) and Ulrich (1999a). In this case mean densities obtained over longer time scales used to fit models of relative abundance will necessarily give a wrong impression about the community structure and their dynamics. We have to treat community structure at every point in time individually.

The above discussion points to the need to rethink the theoretical foundation of mod-

els of relative abundance distribution. The present study undertakes such an attempt. At first we have to look at basic features each animal or plant community has. We then have to establish whether these basic community features lead to distributions of relative abundance. At the end we may try to develop a model that is able to describe these distributions. Such a model will be merely a description of community structure, its parameters may be used as diversity or evenness statistics. We may also derive convenient null-models with which observed patterns may be compared.

2. MATERIALS AND METHODS

2.1. BASIC FEATURES OF SPECIES COMMUNITIES

If we look at real larger communities of animals we may detect three main features that are connected with species body weight:

1. In nearly all communities there is a certain relation between the number of species and their body weight (the species – weight distribution, SWD). Most species have intermediate body weights and the body weight distribution in the majority of taxa is modal (Van Valen 1973, May 1978, Maurer *et al.* 1992, Ulrich 1999b). There are fewer very large and very small species. Fig. 2 shows such a distribution for a hypothetical community of 200 species using a plot of species number against $\log_2$-body weight class. Recently, Novotny and Kindlman (1996) studied this relation in arthropods. They found nearly always a modal distribution of a normal or log-normal shape that was in the majority of cases (17 out of 23)
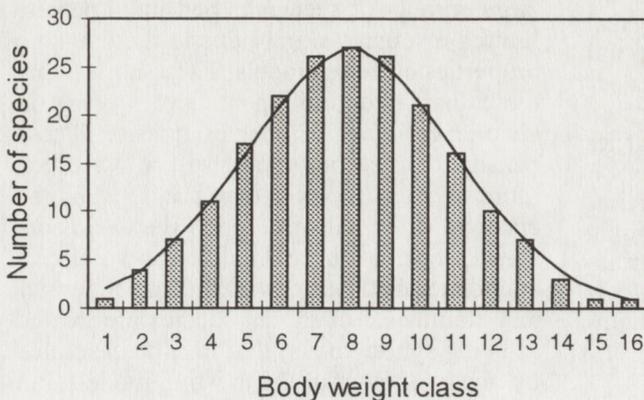

Fig. 2. Species – weight distribution (SWD) of a model community with 16 binary weight classes (mean = 8, variance = 3) and 200 species.

slightly to moderately positively skewed. The number of (binary) weight classes in natural communities may vary considerably. From published data (May 1978, Peters 1983, Rosenzweig 1995) it seems that in general this number will not exceed 30 equivalent to a maximum body size difference from the smallest to the largest species of 9 orders of magnitude. Larger natural insect communities span typically over 10 to 16 binary weight classes (Ulrich 1999b and unpubl.).

2. Mean abundance and body weight are connected (abundance – weight distribution AWD). There is a long discussion about the exact shape of this relation (Lawton 1989, 1990, Currie 1993, Currie and Fritz 1993, Cyr et al. 1997) but in nearly all cases plots of abundance versus body weight look like in Fig. 3. There is a negative regression of log abundance on log body weight with a marked upper boundary in abundance. Often the shape is more or less triangular. The regression is far from being perfect but abundances generally fell inside the areas marked in Fig. 3. In a previous paper (Ulrich (1999c) I argued that such distributions may stem from typical species – weight distributions together with random density fluctuations. Cyr et al. (1997) showed that for a large number of taxa the regression between abundance and body weight could be described by a power function with slope values between 0.5 and 1. The upper boundary however may have a slope from zero (no depend-

ence) to more than 2 (Cotgreave et al. 1993, Hendriks 1999, Ulrich 1999b).

3. All species fluctuate in density. These fluctuations may be chaotically or regular. In the latter case a density dependent process may describe them. However, if we deal with a many species community and the absence of strong environmental forces like physical or climatic stress, their densities will largely fluctuate independently. Every sample from this community refers then to a short time frame and independent density fluctuations then makes a random model where densities are assigned by random numbers suited to describe species densities at this time.

In general, we may identify four types of randomness. Over a longer time scale all densities inside a certain upper and lower boundary may achieve the same probability. In this case a linear random number is able to describe density fluctuations. This is shown in Fig. 4 A. All densities have the same probability. If intermediate densities are more probable than very high or very low ones we may apply a model with a normal distributed random number (Fig. 4 C). There may be a situation, that a species has large density fluctuations but only seldom reaches higher densities. In this case the process may be described by a model that uses linear or normal random numbers on a log scale (Fig. 4 B, D). In this case lower densities are more probable than higher ones. An often-used measure of temporal variability is the coefficient of variation
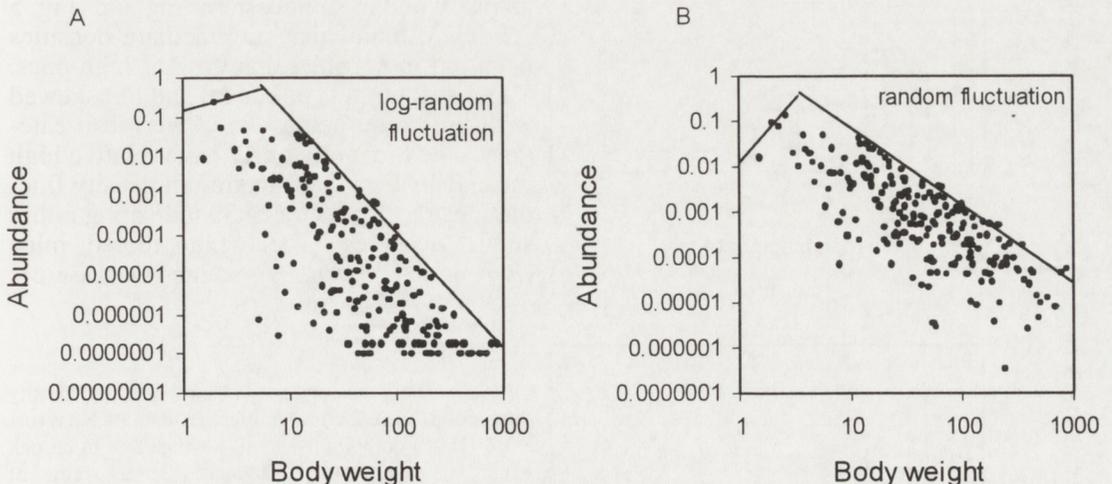

Fig. 3. Abundance – weight distributions (AWD) of 2 model communities with 200 species each and a SWD as in Fig. 2. A: abundances were assigned with random numbers on a logarithmic scale; B: abundances resulted from random numbers on a linear scale.
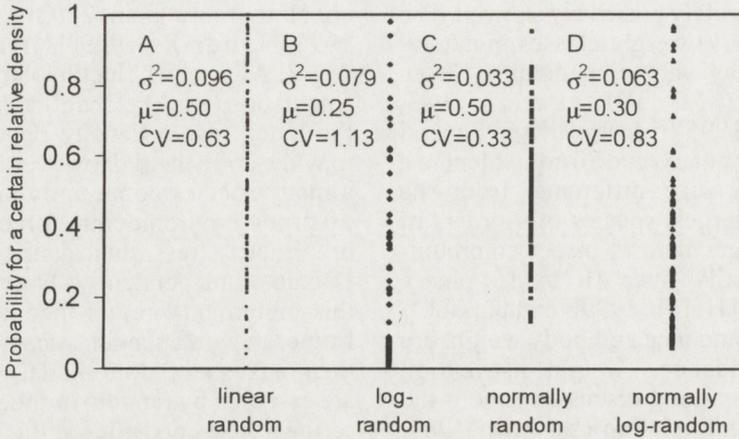
Fig. 4. Four types of randomness. A: linear random numbers on a linear scale resulting in an even probability distribution of densities; B: linear random numbers on a log-scale resulting in a higher probability of having lower densities; C: normal distributed random numbers on a linear scale resulting in a higher probability of having an intermediate density; D: normal distributed random numbers on a log-scale resulting in a higher probability of having intermediate densities at the lower density range. s and m are variance and mean of the distributions, respectively, CV is the associated coefficient of variation.
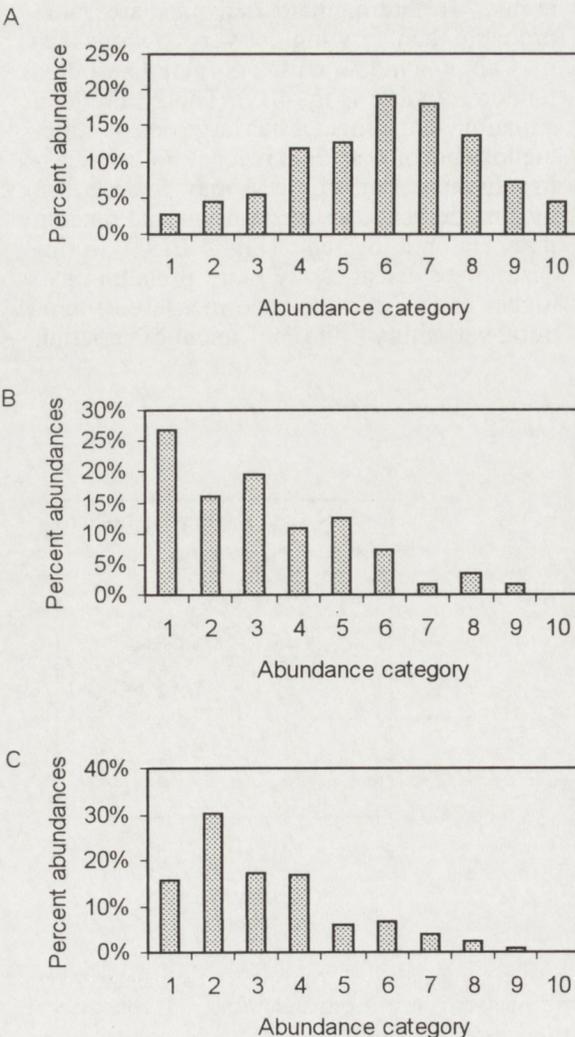
CV (the relation between standard deviation and mean density). Fig. 4 shows that communities whose species fluctuate as in case B and D have generally larger coefficients CV than communities with species fluctuating as in A and C irrespective of the actual range of densities.

Studying temporal variation in natural assemblages needs data of many generations and there are only very few such long term studies. Nearly all of them stem from mammalian and bird surveys (Micheli *et al.* 1999). Fig. 5 gives three examples of them. Newton *et al.* (1998) studied bird species in an oak wood in southeastern England (Fig. 5 A). They found that intermediate densities occurred more often than low or high ones. The distribution is unimodal and left skewed with the mode being above the mean category. The birds obviously have relative high mean densities; their maximum density fluctuations reach a factor of 30 indicating rather stable densities. The white footed mice (*Peromyscus leucopus*), studied by Lewel-

Fig. 5. Three examples of patterns of density fluctuations in real communities. A: data of Newton *et al.* (1998) on abundances of bird species in an oak wood in southeastern England; B: a study of Lewellen and Vessey (1998) on the white footed mice (*Peromyscus leucopus*); C: data of Pollard (1991) of two British butterflies. In every case the abundance data were transformed into 10 equal abundance classes.

len and Vessey (1998), fluctuated to a much larger extent and its modal density is below the mean density category (Fig. 5 B). The distribution is right skewed but again the lowest density classes occur less often. Pollard (1991) followed density fluctuations of two British butterfly populations and a recalculation of his data (Fig. 5 C) showed that most of the time these species had rather low densities but high densities or even outbreaks in certain years. Such a pattern is well described by model B in Fig. 4.

From the available data it seems that the type of density fluctuation may be connected with the r-K continuum of Southwood (1977) and Greenslade (1983). K-selected species (mostly vertebrates) exhibit often density fluctuation as in Fig. 4 A or C. Their range of densities is comparably small with intermediate densities frequently being more probable than very low or very high ones. r-selected species (mostly arthropods) with a high reproductive potential have larger density fluctuations but more often times of relative rarity (Ferriere and Cazelles 1999). Models B and D of Fig. 4 may well describe this pattern.

2.2. COMPUTING PROCEDURES

If we take communities with the features described above, what types of relative abundance distribution do we expect? To answer this question I computed 43 model communities with 20, 50, 100, and 200 species. Normal species – weight distributions as in Fig. 2 with 3, 16 and 30 binary weight classes (octaves) were used (according to features 1 and 2 above). The abundance – weight distributions had slopes of -0.5, -1.0 and -2.0. Table 2 gives all parameter values used for computation.

In a next step each species was assigned a density either by a random process using linear or normal random numbers on a linear scale (as in Fig. 5 A and C)(Fluc = lin in Fig. 6) or by a random process on a log-scale (as in Fig. 5 B and D)(Fluc = log) or by a mixture of both (Fluc = mix) where half of the species followed each of these types (Table 2). This process refers to the feature 3 of natural communities discussed above. The whole process resulted in typical abundance – weight distributions as in Fig. 3.

The resulting relative abundance distributions were then fitted by published models (Table 1): the power fraction and random as-

Table 2. Parameter settings used to generate the model communities of Figs. 2, 3, 6, and 7. n rnd: normal random (Type C in Fig. 4); n rnd log: linear random on a log scale (Type D in Fig. 4); l rnd: linear random (Type A in Fig. 4); l rnd log: linear random on a log scale (Type B in Fig. 4); Mixture: Mixture of the above types where half of the species each followed the above two types of density fluctuation

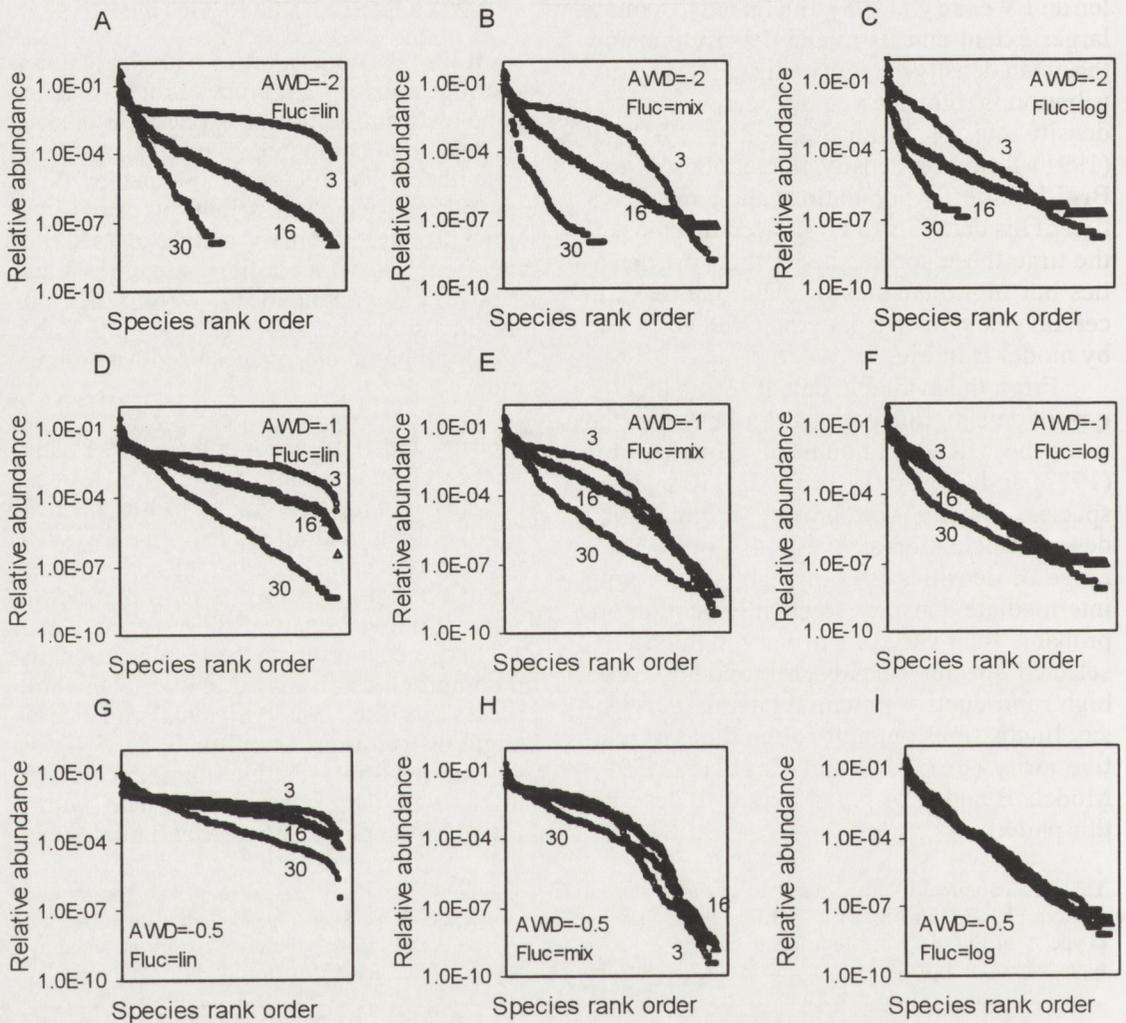| Model community	Species weight distribution (Fig. 2)			Slope of upper boundary of the abundance – weight distribution (Fig. 3)		Type of density fluctuation		Number of species
	Weight classes	Mean	Variance	Mean	Variance			
1	3; 16; 30	2; 8;15	0.5; 3; 10	0.5	0.2	l rnd	n rnd	200
2	3; 16; 30	2; 8;15	0.5; 3; 10	0.5	0.2	l rnd log	n rnd log	200
3	3; 16; 30	2; 8;15	0.5; 3; 10	0.5	0.2	Mixture	Mixture	200
4	3; 16; 30	2; 8;15	0.5; 3; 10	1	0.2	l rnd	l rnd	20; 50; 100; 200
5	3; 16; 30	2; 8;15	0.5; 3; 10	1	0.2	l rnd log	l rnd log	20; 50; 100; 200
6	3; 16; 30	2; 8;15	0.5; 3; 10	1	0.2	Mixture	Mixture	20; 50; 100; 200
7	3; 16; 30	2; 8;15	0.5; 3; 10	2	0.2	l rnd		200
8	3; 16; 30	2; 8;15	0.5; 3; 10	2	0.2	l rnd log		200
9	3; 16; 30	2; 8;15	0.5; 3; 10	2	0.2	Mixture		200

Fig. 6. Relative abundance distribution of model communities of 200 species each with the parameter setting as in Tab. 2 (communities 1 to 9). Given are the slopes of the Abundance – weight distributions (AWD) and the type of random number used to assign abundances (Fluc = lin: linear scale, Fluc = log, logarithmic scale, Fluc = mix = mixture of both). The numbers at the data points refer to the number of binary weight classes of the community.

sortment models of Tokeshi (1990, 1996), the sequential breakage model of Sugihara (1980), and a classical log-normal. Fitting was done with FORTRAN program Frequency distribution that uses a least-square algorithm for fitting and is already described in Ulrich (2001a, b). For comparisons of RADs with linear type density assignment (Fluc = lin) the power fraction model was used due to its flexibility and the fact that it depends on only one shaping parameter k ranging from $-\infty$ to $+\infty$. The higher the value of this parameter the more even is the distribution. For RADs generated with densities assigned at a logarithmic scale (Fluc = log)

the random assortment model of Tokeshi (1993) was used. Here the single shaping parameter k ranges between 0 (most even distribution) and $+\infty$ (maximally uneven).

3. RESULTS

Fig. 6 shows expected relative abundance distributions (RADs) for communities of 200 species under different regimes of density assignment and SWD-weight classes. The shape of the resulting RADs depended mainly on the type of density assignment and the DWD slope. The steeper the slope, the
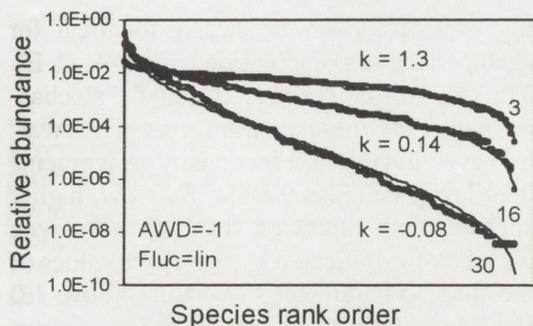
Fig. 7. The communities of Fig. 6 D fitted by the power fraction model of Tokeshi (1996). The k-values refer to the shaping parameter of the model. A power fraction model with $k = 0.1$ would be smiliar to a canonical log-normal, with $k = 1.0$ to a broken stick model. Abbreviations as in Fig. 6.

more unequal were the resulting RADs. Random density assignment at a linear scale (Fig. 6 A, D, G) resulted irrespective of the AWD slope in a pattern that may be described by one of the classical relative abundance distributions of the sequential breakage or log-normal type with a few very abundant and very rare species. For the communities of Fig. 6 D this is shown in Fig. 7. The community with three weight classes is fitted by a power fraction RAD with a shaping parameter k of 1.3. That means that this community has a slightly more equal distribution than expected from a classical broken stick distribution (in this case k would be exactly 1). At 16 binary weight classes a power fraction with $k = 0.14$ fits best. The distributions are unsymmetrical in respect to a higher number of very rare species. This is exactly the pattern that had been found in real large vertebrate communities (Nee et $al.$ 1991, Gregory 1994). More weight classes result in distributions

with log-series tales found in many samples from larger insect communities (Hughes 1986, Novotny and Basset 2000, Ulrich unpubl.).

Currie (1993), Currie and Fritz (1993), and Cyr et $al.$ (1997) showed that for vertebrates the upper slope of the abundance – body weight regression is about –0.9. The theoretical considerations of Griffiths (1992) pointed to a value of –1.0. From this we may predict the community structure of a typical vertebrate community. It should follow relative – abundance distributions similar to Fig. 6 D and depend mainly on the number of binary weight classes. But there is not a single distribution like the canonical log-normal or the sequential breakage (Sugihara 1980) that may serve as a general null model.

Random density assignment at a logarithmic scale (Fig. 6 C, F, I) results in distributions that are neither described by sequential breakage nor by geometric or log-series type distributions. They are characterised by a small number of abundant species and a log-series tale. Mixed types of density fluctuations gave untypical hump-shaped distributions that had up to now not been reported from natural communities.

Figs 6 and 7 used linear random numbers to assign densities. If intermediate densities are more probable than very high or very low ones we have to use normal distributed random numbers. In Fig. 8 the same settings as in Figs 6 D, E, and F were used but with normally distributed random numbers. The general effect of them is that the resulting RADs are more even. The lower curvature of very rare species is also less pronounced. Again a mixed logarithmic – linear regime of density
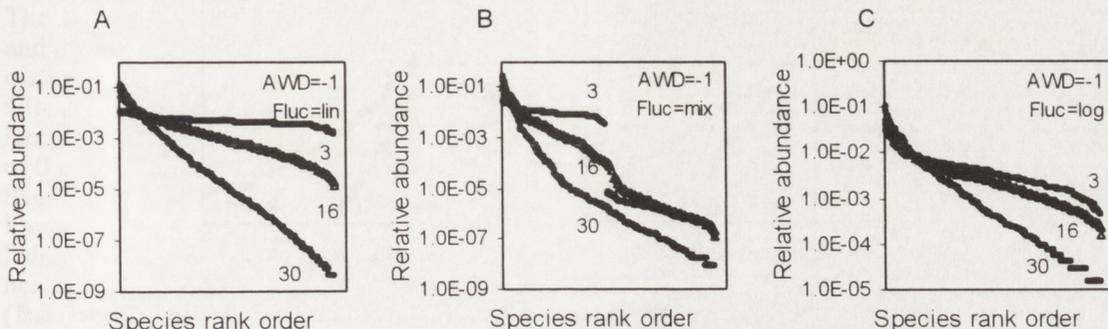

Fig. 8. Relative abundance distributions of model communities with parameter settings as in Fig. 6 D, E, F. Instead of linear random numbers normal distributed random numbers were used to assign densities. Abbreviations as in Fig. 6.

fluctuations gave highly untypical or even broken distributions.

Fig. 9 shows that not only weight related distributions influence the shape of RADs but that the species number itself might determine their shapes. For Fig. 9 six combinations of species weight distributions and density assignments were computed, each time for 20, 50 and 100 species. In the case of linear random numbers (Fluc = lin) shape of distribution and species number are largely independent. I fitted each distribution by a power fraction model and the resulting shap-

ing parameters k were nearly identical for each parameter combination (Fig. 9 A, C, E). The small differences result from the stochastic nature of these distributions. This was, however, not the case for density assignments on a log scale (Figs 9 B, D, F). Now, higher species numbers always result in more even distributions indicated by the lower values of the shaping parameter k; k-values above 1.0 indicate distributions being more uneven than a classical niche pre-emption distribution (Tokeshi 1990).
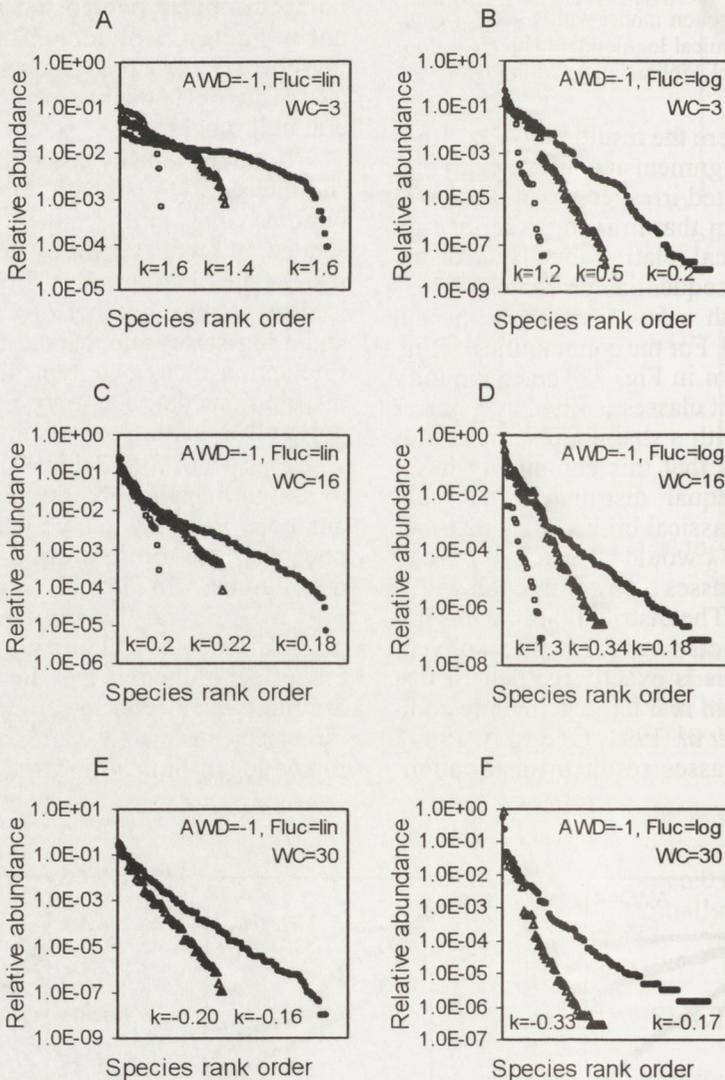

Fig. 9. Relative abundance distributions of model communities of 20 (open circles), 50 (open triangles) and 100 (filled circles) species. Abbreviations as in Fig. 6. The k-values in A, C, E refer to the shaping parameters after fits of the power fraction model, the k-values in B, D, F refer to the respective parameters of fits of the random assortment model of Tokeshi (1990) modified by Ulrich (2001a) (see Tab. 1). In the latter case smaller k-values indicate more even relative abundance distributions with a k-value of 0 referring to the case where all species have the same abundance.

4. DISCUSSION

The distribution of relative abundances in a community of plants or animals at any given time depends not only on complicated processes of niche apportionment but on temporal variability of densities and on body weight related patterns. Classical (Preston 1962, Sugihara 1980) and recent (Tokeshi 1996, Bell 2000, Moulliot *et al* 2000) models of relative abundance distributions ignore the latter dependencies or treat them only as stochastic noise that has to be levelled out by using longer and longer time series and larger sample sizes. Such a view gives a wrong impression about community structure and their variability in time. Variability itself (that means the dynamic properties of communities) shapes community structure and lets species to coexist beyond the boundaries of classical niche dimensions (Leibold 1995, Austin 1999, Huisman and Weissing 1999).

The present paper tries to incorporate temporal variability and to examine what types of relative abundance distribution result if we start from a few basic features of each natural community. These features are body weight related indicating that future models that try to explain RADs have to incorporate patterns of resource use but also patterns of body weight distributions.

An important result of the present paper is that there will be no single relative abundance distribution that is expected for a large non-interactive community. Older (Preston 1962, May 1975, Pielou 1977) and newer (Hubbell 1997, Nummelin 1998) theory often refers to a canonical log-normal as being expected in such communities although this had long been a matter of dispute (Ugland and Gray 1982, Nummelin 1998). The log-normal then served as a null model and deviations were interpreted as induced by disturbance factors or competition (Gulliksen *et al.* 1980, Preston 1980). This prevalence stems from the fact that the derivation of the log-normal by May (1975) simply and uncommented relies on random numbers on a linear scale (the central limit theorem). Published compilations of fits of the log-normal nearly always used vertebrate communities (Preston 1962, Sugihara 1980, Tokeshi 1996). Such communities should have comparably smaller ranges of densities than for instance arthropod communities and density fluctuation patterns as in Figs 4 A and 5 A.

For them May's derivation might apply and Fig. 6 shows indeed a log-normal type pattern. However, Fig. 6 also shows that a log-normal pattern will not be a universal feature of larger communities. For communities whose members exhibit other types of temporal variability with more phases of relative rarity (Kunin and Gaston 1997, Ferriere and Cazelles 1999) other patterns of relative abundance also are expected. These patterns should be similar to the ones of Figs 6 C, F, I.

The present results make it also improbable that a single null-model distribution of the log-normal type exists. Even using parameter values for abundance – weight and species – weight distributions that are expected from recent surveys (Novotny and Kindlman 1996, Cyr *et al.* 1997) (Fig. 6 D) let to different RADs depending on the pattern of density assignment and the species number (Figs 6, 8, 9). Especially the number of weight classes appeared to be decisive. The larger the body weight difference from the smallest to the largest species was, the more uneven was the resulting RAD. However, it is interesting to see (Fig. 9) that a canonical log-normal or Sugihara's sequential breakage model require at least 16 weight classes to fit. For lower numbers of weight classes more even distributions than predicted by classical theory are expected. In his respects it seems worthwhile to reanalyse existing studies on relative abundance distributions and to compare them with respective body – weight distributions.

The present results also indicate that there might be fundamental differences in relative abundance distributions between communities made up of species following a K-selection and a r-selection strategy. The first group contains species with small to moderate (often density dependent) density fluctuations. From Fig. 6 we expect for such communities RADs that can be described by log-normal or Sugihara type distributions with small numbers of very abundant and very rare species. Because of the flexibility of the model such communities may be best described (but not explained) by Tokeshi's power fraction model (Tokeshi 1996). In two recent papers (Ulrich 2001a, b) I showed that the shaping parameter k of this model might be used as a general index of evenness.

Communities made up of r-selected species are not expected to follow such a model.

They should lack the lower curvature of rare species and exhibit a log-series tale. This pattern is very often found in samples of large arthropod communities (Hughes 1986, Morse *et al.* 1988, Novotny and Basset 2000, Ulrich 2001c) and mostly explained by insufficient sampling resulting in the famous veil-line first described by Preston (Preston1962, Nee *et al.* 1991, Ulrich 2001c). The picture of Fig. 6 however indicates that this might not be a sampling artefact but a real feature of animal communities that are characterised by large and chaotic density fluctuations. Up to now the few studies and comparisons of relative abundance distributions did not differentiate between communities of different evolutionary strategies (Sugihara 1980, Tokeshi 1996) or even mixed up species of different types (Hughes 1986). It would be worthwhile to reanalyse existing compilations in this respect.

Fig. 9 showed that all things being equal, a relative abundance distribution may depend solely on the number of species. This notion may have important consequences for indices of evenness and diversity (Ulrich 2001b, d). They all use relative abundances of species for computation. By definition, communities of the same structure, expressed by a certain set of relative abundance generating factors, have the same evenness (cf. the latest review by Smith and Wilson 1996 and Ulrich 2001b). All communities following a Sugihara sequential breakage or a broken stick or a dominance pre-emption model (Table 1) should have the same value in a given evenness index. On this definition rely all recent comparisons of evenness indices (Smith and Wilson 1996, Hill 1997, Weiher and Keddy 1999, Ulrich 2001b, d). Fig. 9 shows that this principle may be violated in the case of communities with density fluctuations on a log scale. In this case higher species numbers resulted in communities with more even RADs. Such a pattern would it make necessary either to rethink the current concept of evenness or to reinterpret comparisons of evenness values from communities with different numbers of species. In this respect a recent paper of Wilson *et al.* (1999) deserves attention. They reported that evenness in plant communities is scale dependent with larger scales always resulting in a higher evenness. The authors claimed to have found one of the few universal generalities in plant community ecology. In their study larger scales were also connected (due

to the universal species – area relationship) with higher species numbers (Wilson *et al.* 1998). It may be that this study found the same effect as described in Fig. 9 but discussed it in terms of evenness.

At the end we may come back to the questions asked in the introduction whether it is possible to derive a single model of relative abundance, whether such a model may lead to a general null hypothesis and whether such a model may serve as the basis for a general diversity and evenness statistics? Recently, Bell (2000) studied an immigration extinction model of species allocation. The author argued that such a model might serve as a general null model for the generation of relative abundance distributions. Because the model relied on stochastic extinction and immigration processes using linear random numbers it takes no wonder that he received in sequential breakage RAD patterns as in Fig. 6, with small numbers of abundant and rare species. The fact that a totally different starting point for generating species abundances but using similar patterns of randomness generates identical RADs points strongly to the interpretation that the crucial point for all RAD models is the way to assign relative densities. Silently, all existing models, not only RAD but also metapopulation or predator - prey models assume stochasticity to work at a linear scale. At such a scale the models assign especially "random densities". The above results indicate that other patterns of randomness (especially such at a logarithmic scale) have also to be taken into account. Additionally, work on natural density fluctuations is needed for an appropriate choice of model type.

Of course, from models of species communities we can not definitely derive what factors shape natural communities. The present results however clearly point to the need of a reanalysis of existing community structures and a comparison of them with body weight related patterns. There is also a need to establish how species in real communities fluctuate in density. Then, we can establish whether all natural communities exhibit the basic features identified in this paper and what are the parameter ranges of these distributions. Only such an analysis will lead to a deeper understanding of community structure and to general models of relative abundance. The present results however do not make it very probable that there will be a single model that is able to describe all commu-

nities as has long been thought. Instead, I expect that there will be a set of models and model choice will then depend on patterns of temporal variability and body weight.

5. SUMMARY

This paper shows that recent models of relative abundances like the log-normal model or sequential breakage or niche apportionment models are not able to describe and explain relative abundance distributions found in natural communities because they are derived from a classical niche concept and assume strong past or present interspecific competition (Table 1, Fig. 1). None of them deals especially with temporal variability and functional niche dimensions. The present paper identifies three basic features of natural communities: unimodal species – weight distributions (Fig. 2), abundance weight distributions with more or less marked upper boundaries (Fig. 3), and species density fluctuations that can be modelled by four different random processes (Figs 4, 5). Modelling communities with these basic features (Table 2) resulted in relative abundance distributions that only in part could be described by classical models (Figs 6, 7, 8, 9) but that had shapes often found in samplings from larger natural communities. No single distribution like the canonical log-normal appeared that may serve as a general null-model. The shape of relative abundance distributions was found to depend on the number of species even if all parameter setting of the generating distributions were identical. This indicates that classical evenness indices (that assume independence of species number) may not be appropriate to compare communities with different numbers of species.

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