Comments about some species abundance patterns: classic, neutral, and niche partitioning models

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(With 4 figures)

Abstract

The literature on species abundance models is extensive and a great deal of new and important contributions have been published in the last three decades. Broadly speaking, one can recognize five families of species abundance models: i) purely statistical or classic models (Broken-stick, Log-normal, Logarithmic and Geometric series); ii) branching process (Zipf-Mandelbrot and Fractal branching models); iii) population dynamics (Neutral models included); iv) spatial distribution of individuals (Multifractal and HEAP models) and v) niche partitioning (Sugihara´s breakage and Tokeshi models). Among these the neutral, the classic and the niche partitioning models have been the most applied to natural communities, the former having been more extensively discussed than the others in the last years. The objective of this paper is to comment some aspects of the classic, neutral and niche partitioning models in a way that the proposed distributions may contribute to the analysis of the empirical patterns of species abundance. In spite of the variety of models, the distributions in general vary between the log-normal and the logarithmic series. From these models the Power-Fraction, together with independent niche dimensions measures, are amenable to experimental tests and may offer answers on which resources are important in the structuring of biological communities.

Keywords: species abundance patterns, neutral models, niche partitioning models, log-normal curve, Power fraction model.

Comentários sobre alguns padrões de espécie-abundância: modelos clássicos, neutros e de partição de nicho

Resumo

A literatura sobre modelos de espécie-abundância é extensa e importantes contribuições têm sido publicadas nas últimas três décadas. De forma geral, são reconhecidos cinco grandes grupos de modelos: i) os que descrevem distribuições puramente estatísticas ou modelos clássicos (Broken-stick, log-normal, série logarítmica e série geométrica); ii) os que simulam processos de ramificação hierárquica (modelos Zipf-Mandelbrot e Fractal); iii) de dinâmica de populações (modelos Neutros); iv) de distribuição espacial de indivíduos (modelos Multifractal e HEAP); e v) de partição de nicho (modelos de Sugihara e de Tokeshi). Os modelos clássicos, os de partição de nicho e principalmente os modelos neutros têm sido os mais utilizados em estudos de comunidades naturais. O objetivo deste artigo é discutir de que forma as distribuições geradas por estes três grupos, bem com as suas bases conceituais, podem contribuir com a análise de padrões empíricos de espécie-abundância. Em geral, estes padrões variam entre as curvas log-normal e série logarítmica. Dentre a variedade de modelos existentes, o Power-fraction possibilita a simulação de uma grande amplitude de padrões de abundância relativa e é de utilização relativamente simples, podendo ser utilizado em testes experimentais de perturbação ou de sucessão ecológica. Aliado a medidas independentes de dimensões de nicho, este modelo pode ainda oferecer respostas sobre quais recursos são essenciais à estruturação de comunidades biológicas.

Palavras-chave: padrões de espécie-abundância, modelos neutros, modelos de partição de nicho, curva log-normal, modelo Power-fraction.

1. Introduction

One of the main objectives in community ecology studies is to verify if foreseeable and persistent structures exist, and to suggest a synthetic theoretical set to interpret the observed patterns (Meffe and Sheldon, 1990; Chave, 2004). The pattern of relative species abundance is an expression of the momentary balance set up within the community, resulting from past and/or present competition for resources, and population dynamic processes (Williams, 1964). This pattern is viewed as the most fundamental aspect of the community (May, 1975) and, according to its measuring accuracy and simplicity can be positioned in an intermediate degree of complexity among other community descriptors (McGill et al., 2007). A mathematical order in relative species abundance is expected, and the frequency distribution of the number of species with different numbers of individuals is probably universally expressed as a hollow-curve type (McGill et al., 2007).

In the last 70 years, a series of studies have been developed aiming to understand this pattern and to generate models that reflect the species abundance distributions empirically observed (Motomura, 1932; Fisher et al., 1943; Preston, 1948; MacArthur, 1957; 1960; Preston, 1962a; 1962b; Caswell, 1976; Sugihara, 1980; Hughes, 1986; Tokeshi 1990; 1996; Bell, 2000; Hubbell, 2001). The initial hope of finding a mathematical model that closely fits observed data based on well established ecological and statistical theory and amenable to further tests and experiments has proved to be a difficult task. So the literature on this theme has become extensive, with a great number of new contributions appearing in the last three decades.

Recently McGill et al. (2007) published a thoughtful review on the current knowledge of species abundance distributions (SAD) theory organizing the existing models and theories in well defined groups: purely statistical, branching process, population dynamics, niche partitioning and spatial distribution. Among other contributions, the authors stress the need for future research, calling for advances in theoretical, statistical and field work studies.

SAD gained a renewed attention after the publication of Hubbell´s Unified Neutral Theory (Hubbell, 2001) with a great number of recent published papers discussing the effects of neutral process on this patterns (Borda-de-Agua et al., 2002; Magurran and Henderson, 2003; McGill, 2003; Tilman, 2004; Alonso and McKane, 2004; Magurran, 2005, 2007; Etienne, 2005, 2007; Etienne and Olff, 2005; Walker and Cyr, 2007; Zillio and Condit, 2007). On the other hand, the niche partitioning models remained little explored after the Sugihara and Tokeshi papers (Sugihara, 1980; Tokeshi, 1990; 1996) and except for some field tests (Naem and Hawkins, 1994; Bersier and Sugihara, 1997; Cassey and King, 2001; Fesl, 2002; Mouillot et al., 2003; Johansson et al., 2006; Higgins and Strauss, 2008), only Sugihara et al. (2003) discussed theoretically its close relationship with other ecological patterns.

In this paper we revisit the classical species abundance distributions (geometric series, logarithmic series, log-normal and broken-stick), the neutral and the niche partitioning models. The main parameters to be estimated, and in some cases difficult to interpret, are presented and discussed, as well as the distributions described by each model. The log-normal and the logarithmic series patterns are discussed as predictions of a variety of theories and repeatedly seen in nature. Finally these three groups of models are compared in such a way that the proposed distributions may contribute to the analysis of empirical patterns of species abundance.

2. Classical Species Abundance Models

The first attempt to find a mathematical relationship between the number of species and the number of individuals of a sample was developed by Motomura (1932), resulting in the geometric distribution series. Later, Fisher et al. (1943) developed the logarithmic series. Both were proposed purely as statistical distributions albeit their motivation initially was biological, as they were biologists or Biology related scientists (Williams, 1964). In the four classical models soon to be described, we see that the dominance pattern steadily increases from the broken-stick to the truncated log-normal, logarithmic and geometric series.

2.1. The geometric series

The geometric series (Motomura, 1932) was proposed for benthos communities in lakes. The parameter k of the distribution would be seen as an indication of the species composition complexity in the system. According to Tokeshi (1993), Motomura was just trying to treat the geometric series as a simple description of ecological communities, although subsequent interpretations were contextualized in a process of resource partitioning (May, 1975; Magurran, 2004). From this point of view, the distribution would be described by a situation in which the dominant species uses a proportion k of the whole initially available resource, leaving a fraction (1–k) free. The second dominant species uses the same k fraction of the remaining resource, the third the same fraction k of what was left by the other two, until all species have been inserted as a community. If the abundances are proportional to the total of the used resources, the number of individuals of the i-th species can be expressed by $n_i = NC_k\ (1 - k)^{i-1}$, where n_i is the number of individuals of species i, N the total number of individuals in the community, k the fraction of resources used by each species and $C_k = [1 - (1 - k)^S]^{-1}$, a constant which assures that $\sum n_i = N$. May (1975) discusses that the geometric series represents a situation in which all species are energetically equivalent and that the magnitude of this relationship is proportional to the abundance of the species, where those more abundant require more energy from the system. However as the geometric series is only defined in terms of number of individuals, it does not take into consideration the body size effect in the energy requirements of the species.

2.2. The logarithmic series

The logarithmic series distribution proposed by Fisher et al., (1943) slightly resembles a hyperbole, decreasing as the number of individuals of each species increases and it can be predicted by the expression:

$$\alpha x, \alpha x^2 / 2, \alpha x^3 / 3, ..., \alpha x^n / n \qquad (1)$$

where $\alpha x^n/n$ represents the number of species with n individuals. The value of x is obtained by iteration in the equation $S/N = [(1 - x)/x]*[-\ln(1 - x)]$ and in practice it is located in the interval 0.9-1 (Magurran, 1988; 2004). The constant α is sample size independent and could be used as an index of diversity, remaining robust as such even if the data are not adequately fitted by the logarithmic series (Fisher et al., 1943; Wolda, 1983; Magurran, 2004) As x remains near to 1, α is also a good predictor of the singleton species in the community (Magurran, 2005). Fisher et al. (1943) have shown that all random samples of individuals that form a population distributed as a logarithmic series also present a logarithmic series pattern, having the same α, but with a lower value for x (Williams, 1964).

2.3. The truncated log-normal distribution

The truncated log-normal distribution was initially applied to biological data (Preston, 1948). Putting the species abundances in a histogram in logarithmic scale, the author obtained a curve which adjusted well to a large number of community data. The R classes obtained in the histogram using $\log_2$ were called “octaves”, where each one represents the double of the previous class (1, 2, 4, 8, 16,..., etc). However, any logarithmic scale does the same job (Williams, 1964). It is expressed as:

$$S(R) = S_0 e^{\left(-a^2 R^2\right)} \qquad (2)$$

where S(R) is the number of species of the class R, S_o is the number of species in the modal class and $a = (2\sigma^2)^{-1/2}$ a dispersion constant, inversely related to the standard deviation of the curve.

In population samples the distribution is truncated on the left. The area behind this point represents the species not seen in the sample and tends to reduce as the sample size becomes greater.

In two subsequent papers, Preston (1962a; 1962b) points out a property of the distribution, which emerges when certain demands are satisfied. Plotting in the same graph the number of species in each class (the species curve) and the histogram of the individuals abundance (the individuals curve), the author verified that the modal class (R_{max}) of the first curve overlapped with the modal class (R_N) of the second curve. So

$$R_N \Big/ R_{max} = \ln 2 \Big/ \left[2a \left(\ln S_0 \right)^{1/2} \right] = \gamma = 1 \qquad (3)$$

The resulting curve was called canonical lognormal. In this situation, there are more individuals in the class R_{max} than in any other and the parameter a varies within very narrow limits ($a \approx 0.2$).

2.4. The broken-stick model

MacArthur (1957; 1960) imagined that the niche space could be compared to a stick of length 1, where n–1 points would randomly generate n segments with lengths proportional to the number of individuals of each species in the community. From this the expected abundance of species i would be given by:

$$n_i = N \Big/ S * \sum_{i=1}^{S} \frac{1}{n_i} \qquad (4)$$

where n_i represents the number of individuals of the species i; N the total number of individuals and S the total number of species in the community.

Considering the four classical models, the broken-stick is the only one originally based on biological reasoning describing the process of niche partitioning in a community where the species present continuous and non overlapping niches (Magurran, 2004).

3. Neutral Models

The neutral models are a type of dynamic model (McGill et al., 2007) and treat the organisms in the community as essentially identical in their per capita birth, death, migration and speciation rates. Therefore they do not make any reference to the specific differences in the niche space.

3.1. Caswell model

Caswell (1976) applied the neutral model of allelic frequencies to the species abundance, in order to generate a situation in which the community was completely independent of biotic interactions, and that could be used as a basis to test the intensity of these interactions. In this model, the immigration tax v refers to the arrival of new species, following a Poisson distribution, independent of the number of species already present in the community. The birth and death rates are the same, jointly described by a single parameter. The pattern of resulting species abundance is similar to the logarithmic series, but it tends to the log-normal curve as v increases. However, the log-normal pattern would only be found in the extremely large community samples.

3.2. Bell model

Bell (2000) emphasizes dispersion processes and local establishment starting from a finite group of S species (metacommunity, sensu Hubbell, 2001). From a Monte Carlo simulation, species abundance depends on the parameters m (immigration probability), b (birth rate), d (mortality rate) and K (community’s carrying capacity). If the number of individuals exceeds the carrying capacity, they are removed at random till the community reaches K individuals again. As each individual has the same probability of being removed, the effect on each species is proportional to its abundance.

The community's diversity in the neutral Bell (2000) model is maintained by the immigration process, without which the community would become less and less diverse until there remained only one species. The species abundance pattern foreseen was similar to the log-normal distribution, but it presents a slight negative asymmetry (Figure 1).

When the parameter m is modified, in a way to allow only the immigration of new species, the asymmetry becomes more and more sharp until that the majority of the rare species is composed just by one individual and the pattern resembles the logarithmic series.

3.3. Hubbell model

In the Hubbell (2001) model, the local community is inserted in a regional assemblage, or metacommunity, which defines the scale in which the speciation events occur. Diversity in the local community is maintained by individual migration from this metacommunity (Magurran, 2005; Walker and Cyr, 2007). The model needs the parameter θ, a non-dimensional number which determines the dominance in the metacommunity, and the parameter m, the migration rate or isolation degree which represents the individuals' proportion in the local community, replaced by individuals of the metacommunity. When m = 1, both communities will have the same composition and the same species abundance pattern, similar to the logarithmic series. When m decreases, the local community becomes gradually more isolated, supporting less rare species. This modifies distribution to a log-normal pattern, but still maintaining the negative asymmetry.

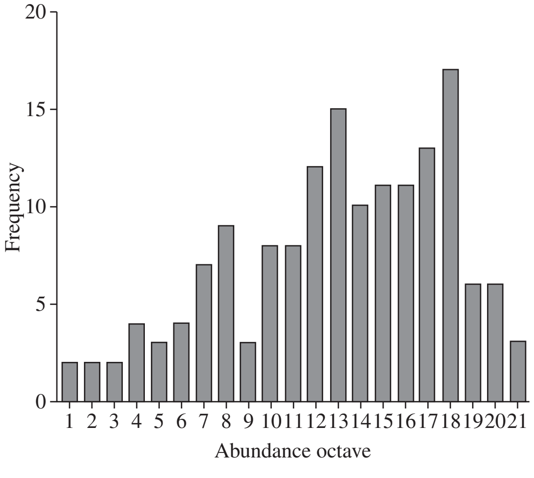

Figure 1. Negative asymmetry in SAD explained by the excess of rare species than predicted by the log-normal model (modified from Bell, 2000).

4. Biological Models of Niche Partitioning

The models of niche partitioning, unlike the neutral ones, foresee communities organized by processes of biotic interactions and are, in essence, similar to the broken-stick model (MacArthur, 1957; 1960). The niche space is broken in fractions proportional to the abundances of the species, with the difference that the partition process is sequential and not simultaneous. This has been seen as a more realistic situation, simulating the species arrived in the community, by ecological or evolutionary events (Sugihara, 1980).

4.1. Sugihara niche-hierarchy model

The main objective of Sugihara (1980) was to offer a biological theoretical background to the canonical log-normal hypothesis. The species abundance distribution would be a consequence of an underlying hierarchy in the community´s niche similarities, and thus, the sequential breakage process described by Sugihara's model would reflect this branching structure (Sugihara, 1989). The relationship between species abundance distributions and dendrograms of niche similarities has only recently been demonstrated (Sugihara et al., 2003). The abundance pattern construction begins with an axis of size 1, the niche space, which will be successively divided. The first division occurs in two parts, with 25 and 75% of the initial size. Soon afterwards one of the two is chosen at random, which again is divided in the proportion 0.25:0.75. The process continues until S relative fractions are formed relative to the community's richness. The model reproduces a species abundance pattern similar to the canonical log-normal curve, but also foresees a slightly negative asymmetry on log scale.

4.2. Tokeshi models

Tokeshi (1990, 1996) developed a series of similar models, in which the choice of the niche fraction to be subdivided depends on the probability p and the breaking point may take place at any position between 0 and 1 (in the model of Sugihara the choice was always random and the division point fixed in 0.25:0.75). The process of the abundance pattern construction follows the outline of Figure 2 and it finishes when S divisions, relative to the number of species in the community, are formed. In these models, the dominance pattern depends on the probability p associated to each niche fraction. The resulted SAD vary from uneven patters like the geometric series to extreme even ones similar to the broken-stick model (Figure 3).

4.2.1. Dominance Pre-Emption and Dominance Decay

In Figure 3a the largest and the smallest dominance patterns are described respectively by the Dominance Pre-Emption and Dominance Decay models. In the first, the arriving species always divides the fraction of the less abundant resource in the community. It is a stochastic model whose expected pattern after several simulations, corresponds to the geometric series with k = 0.75 (Tokeshi, 1990). The Dominance Decay model gener-

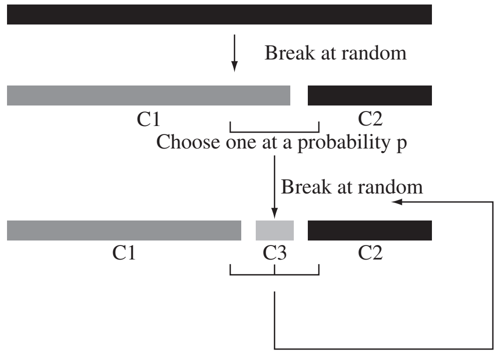

Figure 2. The representation of the construction of a niche partitioning model. Each model differs according to the probability p of choosing the portion that will be divided (modified from Tokeshi, 1999).

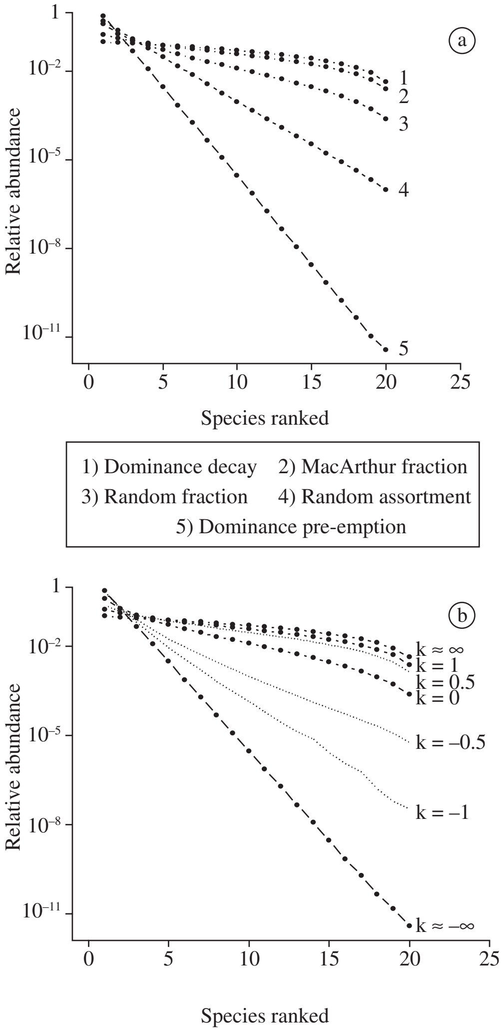

Figure 3. Patterns of species abundance described by the Tokeshi models. a: Dominance Pre-Emption, Random Assortment, Random Fraction, MacArthur Fraction and Dominance Decay. b: Power Fraction model for values of k ranging from – ∞ to + ∞.

ates the most uniform distribution among all the others, assuming that the alien species always divides the resources with the community's most abundant species, an inverse scenario to the previous model.

4.2.2. MacArthur Fraction and Random Fraction

Different from the two previous models, in the MacArthur Fraction and Random Fraction models all fractions have probability of being selected for division. The MacArthur Fraction model is a sequential version of the broken-stick model. To each step, the probability p that a fraction is chosen is proportional to its size, in other words, the species that use larger amounts of resources have more chance of dividing them with the alien species. Tokeshi (1999) interpreted it in an evolutionary context, in which the speciation rate is proportional to the size of the population. In the Random Fraction model the selection probability for successive divisions is independent of the size of the fragment, and so, the amount of resources used by the species does not affect the probability that these are distributed in the community.

4.2.3. Power Fraction

The Power Fraction model offers a different vision for the construction of the relative abundances, in the sense that the chance of a portion to be chosen for division is equal to n_i^k, where n_i is the relative size of the niche or of the portion i (i varies from 1 the S species) and k is a parameter that relates the size of each fragment (amount of available resource) with its chance of being selected for the successive divisions. With k = 0 the probability of a given resource to be chosen does not depend on its size and the pattern results in the Random Fraction. On the other hand, while with k = 1 the abundance distribution is similar to the MacArthur Fraction. In this way, the value of k is a continuous measure determining the community equitability pattern. All Tokeshi models already discussed can be simulated varying k from - ∞ to + ∞, which are extreme cases in which the probability choice is strongly correlated to the size of the portion and they tend, respectively, to the Dominance Pre-Emption and Dominance Decay models (Figure 3b).

4.2.4. Random assortment

This model is slightly different from the others, because it assumes independence among the abundances of the species, an expected situation when the size of the populations experiences stochastic variations controlled by climatic fluctuations. So,

$$N_1 = 1 \text{ and } N_i = r_i N_{i-1}, \text{ for } 2 \le i \le S; \qquad (5)$$

where r is a continuous uniform random variable.

4.2.5. Composite model

The Composite model was proposed as a way of dealing with the situation in that more than one process may be involved in the community's structuring. Basically it is assumed that there exists two (or more)

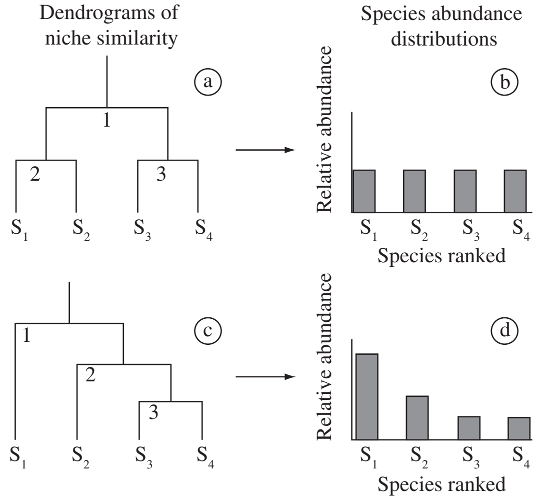

Figure 4. Correspondence between the niche similarity dendrograms and the species abundance distributions (modified from Sugihara et al., 2003).

groups of species and that each one is formed by one of the processes described above. It was originally suggested that the size of the populations of rare species is not structured by biotic interactions, but that it varies independently as expected by the Random Assortment model. In this case, the appropriate model would use the Random Assortment model to describe the pattern for the rare species and some of the others to describe the pattern for the remaining ones of the community.

4.3. Log-series and log-normal curves and negative asymmetry

The description of a log-normal pattern is common to a large number of different communities, but the causes of that is highly controversial (MacArthur, 1960; May, 1975; Sugihara, 1980; Ugland and Gray, 1982; Tokeshi, 1996; Williamson and Gaston, 2005). A common interpretation is that the log-normal curve is a consequence of the Central Limit Theorem. According to MacArthur (1960) the opportunist species growth rate (≈ occasional or rare) would be controlled by environmental independent and stochastic variations, whose multiplicative effects would lead to a log-normal distribution. This would be a particular case in which the variable of interest would represent the abundance of the species, but it would not reflect any biological characteristic helping to understanding the communities' structuring mechanisms. Even the canonical hypothesis would be the expected result for a large group of data controlled by independent factors of multiplicative effects (May, 1975). In another situation, when the assemblages are controlled by biotic interactions, a broken-stick distribution appears (Macarthur, 1960). More recently the stochastic effects acting independently on each single species are believed to generate a distribution similar to a logarithmic series while biotic interaction would lead to a log-normal pattern (Sugihara, 1980; Tokeshi, 1990; Magurran and Henderson, 2003; Ulrich and Zalewski, 2006). If the community is composed of interacting and non-interacting groups, the final pattern is close to the log-normal but skewed to the left (Figure 1), usually interpreted as a result of the excess of rare species (Nee et al., 1991). This pattern has been empirically described for estuarine fishes (Magurran and Henderson, 2003) and for an assemblage of ground beetles (Ulrich and Zalewski, 2006).

The community's division into different groups was also suggested by other authors to explain the negative asymmetry (Ugland and Gray, 1982) as well as the interaction mechanisms in the community (Sugihara, 1980; Tokeshi, 1996). In the niche partitioning models, the negative asymmetry results from the resource division process (Sugihara, 1980; Tokeshi, 1996) and so, it would not be necessary to suppose that the rare species compose a community's non-interactive portion. The Random Fraction, Power Fraction (for values of k close to zero) and Sugihara's niche breakage models describe very similar patterns (Tokeshi, 1999). Among these, the Power Fraction model deserves attention, as it allows that small variations in the parameter k alter the degree of asymmetry of the distribution.

The neutral models also predict this asymmetrical log-normal pattern, although in these, the abundance of rare species depends on the migration intensity between the metacommunity and the local community. If the immigration process increases, the skewed-to-the-left log-normal changes in direction to a logarithmic series distribution (Bell, 2000; Hubbell, 2001).

Based on Monte Carlo simulations, McGill (2003) suggested the log-left-skew could emerge as a result of an increasing in sampling effort or from a sum of many temporal or spatial autocorrelated data sets, and so, caution is needed in quantifiyng and interpreting this characteristic biologically.

Although theoretically the logarithmic series and the log-normal patterns are a consequence of different mechanisms, empirically they are difficult to be distinguished (Mouillot and Wilson, 2002). As is expected, in a sampled community the majority of the rare species are missing and even if the population is log-normal distributed, the resulting pattern is the truncated log-normal (Preston, 1948). The problem with the truncated log-normal is that it is indistinguishable from the logarithmic series if the median is before the truncation point (Magurran, 2004). Actually, these two classic patterns like the geometric series and the broken-stick ones are basically used as reference patterns for other mechanistic models which go beyond the statistical description.

4.4. Observed patterns and causal mechanisms

In the last 30 years, an inversion in the focus has been observed, where the models evolved from the simple description of the patterns of relative abundance to the simulation of causal processes based on ecological theories of community organization. The relevant point is that starting from different processes the same patterns were arrived at, and so, the simple adjustment of the data to a model does not necessarily implicate in the acceptance of its theoretical background (McGill et al., 2007). This acceptance depends, above all, on a priori scientific judgment of how realistic are their premises, although indeed, these cannot be tested.

After the publication of Hubbell's neutral theory (Hubbell, 2001), a great deal of attention has been given in reconciling two apparently opposed niche and neutral theories of community organization. The first rests on the concept of ecological niche (Hutchinson, 1957) and the principle of competitive exclusion (Hutchinson, 1965). They sustain that the niche space of the species should present a minimum overlap in order to lessen the resource competition effects allowing coexistence in the community. Following this principle, the broken-stick model (MacArthur, 1957; 1960) predicts the abundance pattern for a community in equilibrium completely structured by processes of resource division. The second one, the theory of neutrality, sustains that the factors that maintain the community well structured are mainly related to the dispersion processes, speciation, birth and mortality rates (Caswell, 1976; Bell, 2000; Hubbell, 2001).

As usually happens when two opposed ideas are in debate, several authors suggest that one should seek for a formulation that sets out the processes proposed in both theories, aiming to arrive at a "quasi-neutral" theory of biodiversity (Sugihara et al., 2003; Tilman, 2004; Chave, 2004; Gaston and Chown, 2005; Gewin, 2006; Clark et al., 2007; Zillio and Condit, 2007). The stochastic niche theory (Tilman, 2004) proceeds in this sense although it privileges resource consumption (Zillio and Condit, 2007). This model simulates the process of the community's construction and possesses a complex formulation aiming above all, to analyze conceptual theoretical ecology matters. Models which propose the fitting to empirical data should be simpler and, therefore, more general in their predictions.

Hubbell's (2001) neutral model only needs to estimate two parameters (m and θ). Recently Etienne (2005) proposed a new probability function and a new algorithm to obtain the maximum likelihood estimates of the parameters m and θ. However for large data sets, the algorithm takes time to build the abundance distribution and so, Walker and Cyr (2007) suggest a quicker approximative method. In both cases, the algorithms are relatively complex.

In comparison, the niche partitioning models have received much less attention but even so, they deserve some important comments. Although these models do not generate predictions beyond the SAD per se (McGill et al., 2007) and treat more abstract process than population dynamics models (neutral ones included), they are relatively easy to implement, can be applied to various types of abundance measures (number of individuals, biomass or cover) and are amenable to more simple tests like experimental perturbations. In general ecology, experimental tests are the more direct way to link the observed patterns and the causal process involved. Considering the theoretical expectation of increasing equitability patterns following the natural succession in community organization (Harvey et al., 1983), the Power Fraction model allows several species abundance patterns between the extremes of dominance (≈ geometric series) and uniformity (≈ broken-stick) just by adjusting the parameter k. Until now, the Tokeshi resource partitioning models have only been applied to parasites communities (Naeem and Hawkins, 1994; Mouillot et al., 2003), dragonflies (Johansson et al., 2006), beetles (Ulrich and Zalewski, 2006), birds (Bersier and Sugihara, 1997), chironomidae (Tokeshi, 1990) and stream fishes (Higgins and Strauss, 2008). The process of community building is done without great mathematical or computational difficulties, making them an accessible analysis tool to most scientists. The program PowerNiche (Drozd and Novotny, 2000), developed in Excel® allows the expected values of abundance for each model to be obtained, but with a limited number of simulations. Probably protocols to test the goodness of fit (Bersier and Sugihara, 1997; Cassey and King, 2001; Mouillot et al., 2003) will soon be inserted into some computational interface for easy using.

The assumptions of these models determine that there exists a fairly linear relationship between species abundance and niche width. The chance of each species to share their resources with the alien species, in some way, is a function of its abundance. The association between abundance and niche width (Brown, 1984) assumes that the species that compose the current community have been able to maintain their populations along an evolutionary process, which tended to optimize the relationship between the niche requirements and resource availability (Tokeshi, 1999). On the contrary, if the objective is to differentiate communities regarding more recent ecological effects (human induced impacts or species introduction), it is preferable to interpret abundance as reflecting the immediate use of the available resources. There is a debate as to whether the individual´s species abundance would appropriately reflect biomass or energy distribution among species at the community level (Harvey and Godfray, 1987; Sugihara, 1989; Pagel et al., 1991; Taper and Marquet, 1996). Pagel et al. (1991) demonstrated that this relationship can vary depending on the situation, but in the majority of the communities analysed, the energy and biomass species abundance distribution was a little bit less equitable than individual species abundance distribution. Tokeshi and Schmid (2002) recognized that the relationship between niche width and abundance is just an approach assuming that specific differences in the way of obtaining the resources may distort it. The general recommendation of Tokeshi (1993) is to use species biomass to describe the sequential resource apportionment processes, mainly when the body size is too variable in the community.

Several articles on the biological models of niche partitioning emphasize the simulation processes (sequential division and probability of choosing the fragment), which is essential for the correct understanding of the mechanisms, but on the contrary, little is commented on the ecological causes that lead the alien species to compete for the largest or smaller fraction of resources (Tokeshi, 1990; 1993; 1996; Tokeshi and Schmid, 2002).

Recently Sugihara et al. (2003) proposed a conceptual outline that would allow to link up SAD to the dendrograms of niche similarity (Figure 4). Assemblages organization would depend on a simple rule of hierarchical organization, understood as the final product of multiplicative effects, where the species would compete predominantly inside the guilds. These guilds could be identified in grouping dendrograms, usually related to a niche dimension (ecomorphological space, feeding or reproductive patterns). The authors foresaw that isolated species in groups less subdivided in the dendrograms would be more abundant, as they would use a portion of resources unavailable to a majority of the species in the assemblage. So this concept does not implicate in competition occurrence among all species, like other niche partitioning models do. To confirm these forecasts, eleven documents (papers or unpublished theses) were analysed, that could offer independent measures of species abundance and niche similarity. From the eleven analysed communities including fish, amphibians, reptiles and birds, ten confirmed the forecast.

The model suggests that drastic, recent and human-induced disturbances (e.g., deforestation) would increase or reduce disproportionately the availability of some resource (e.g., the luminous intensity or nutrient availability), favouring one or few groups to the detriment of the others. The species in these groups would become dominant, generating more heterogeneous abundance patterns, which clearly defines an estrangement of the equilibrium condition in the assemblage as a whole. To the contrary, in an environment in which there is a great variety of resources, the species would be maintained in a closer condition to the equilibrium, coexisting in more uniform abundance patterns.

Although the concept of Sugihara et al. (2003) underlies the branching process of species competing within the guilds, in essence, it does not differ from the relationship already expected between the equitability patterns and the community organization processes (May, 1975; Harvey et al., 1983). With little conceptual modifications, this model can be allied to another niche partitioning model, the Power Fraction (Tokeshi, 1996), allowing us to compare the structure of the assemblages without the need of making inferences on discrete patterns of resource use (like the other Tokeshi models) and still to confront them with overlap measures of feeding, of reproductive traits or of the ecomorphological space use, when available. So it is possible to assess the importance of these attributes, positioning the assemblages along ecological gradients related to the patterns described by the dendrograms of niche similarity and the species abundance distributions.

The value of k tending to $-\infty$ would describe a situation in which a great deal of the resources would be available to few species, generating a highly dominant pattern, which would only happen in extremely poor or degraded environments. In an opposite situation, when the value of k would tend to $+\infty$ the assemblage would be composed of several ecological groups, each one of them equally rich and diverse in relation to the species composition. In this case, no group would become exaggeratedly abundant and the SAD would be as uniform as predicted by the Dominance Decay.

When considering community hierarchical organization (Sugihara et al., 2003) together with the Tokeshi models, mainly the Power Fraction, it is possible to tie up general conceptual questions about the niche theory to empirical analyses of SAD and to independent measures of niche dimensions, making inferences about which resources are fundamental in assemblages structuring. Using the parameter k of the Power Fraction model, the analyses become sensitive to subtle differences in SAD that cannot be assessed with the other niche partitioning or with the classic models. Special attention must be given to experimental perturbations tests and natural or anthropic gradient analyses. So, even if they provide a peculiar view of the structuring mechanisms, the merit of the resource partitioning models lies in the generality of their assumptions and in the simplicity of their use. These are welcome characteristic in an area of the community ecology that needs, at the same time, to supply accurate predictions and to develop simple and efficient tools for data analysis.

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