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Analyzing fractal property of species abundance distribution and diversity indexes



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HIGHLIGHTS

• This study constructs a new model of SAD based on fractal theory.

- This model has a good fit to SADs of 104 community samples from 8 taxonomic groups.
- The significance of the fractal parameter relates to the "dominance" of a community.
- This work combines diversity indexes and SAD into a broader perspective of diversity.

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ABSTRACT

Community diversity is usually characterized by numerical indexes; however it indeed depends on the species abundance distribution (SAD). Diversity indexes and SAD are based on the same information but treating as separate themes. Ranking species abundance from largest to smallest, the decreasing pattern can give the information about the SAD. Frontier proposed such SAD might be a fractal structure, and first applied the Zipf–Mandelbrot model to the SAD study. However, this model fails to include the Zipf model, and also fails to ensure an integer rank. In this study, a fractal model of SAD was reconstructed, and tested with 104 community samples from 8 taxonomic groups. The results show that there was a good fit of the presented model. Fractal parameter (*p*) determines the SAD of a community. The ecological significance of *p* relates to the "dominance" of a community. The correlation between *p* and classical diversity indexes show that Shannon index decreases and Simpson index increases as *p* increases. The main purpose of this paper is not to compare with other SADs models; it simply provides a new interpretation of SAD model construction, and preliminarily integrates diversity indexes and SAD model into a broader perspective of community diversity.

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1. Introduction

Community diversity is essential to theoretic and applied ecology (Pielou, 1975). However, a community's diversity index is merely a single descriptive statistic, noting that community diversity also depends on the species abundance distribution (SAD) (Simpson, 1949; Mouillot et al., 2000). A SAD is a description of the abundance for each different species encountered within a community (McGill et al., 2007). Since the exact nature of SADs can provide a basis for full understanding of community structure (Pielou, 1975), the study of SAD always lies at the heart of community ecology (Tokeshi, 1993).

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http://dx.doi.org/10.1016/j.jtbi.2015.12.010 0022-5193/© 2015 Elsevier Ltd. All rights reserved. The definition of SAD is the number of species within a specified abundance class in the community or sample. When a community only has a few species, it is customary to rank species abundance from largest to smallest; that is, the SAD is presented in a rank-abundance diagram with the rank (r) on the abscissa and relative abundance (F_r) on the ordinate (Pielou, 1975; McGill et al., 2007). Thus, the monotonically decreasing pattern (either linear, or convex, or concave, or with steps, etc.) gives a lot of information about SADs (Frontier, 1987, 1994).

Any description of the SAD is worth interpreting, and will be more meaningful if it is accompanied by a mechanistic understanding of the processes involved (Tokeshi, 1993). Frontier proposed that the SAD might be a typical fractal structure (Frontier, 1985, 1987, 1994; Mouillot et al., 2000). "Consider the classical construction of any fractal object by indefinitely repeating a generating process. At any step of the generation, *K* auto similar

Table 1

SAD fractal structure of Zipf–Mandelbrot model. Numbers of new species (N_i) and its relative abundance (F_i) during ecological succession (Frontier, 1994; Mouillot et al., 2000).

Successive steps, i	Number of new species, N_i	Relative abundance, F_i
1 2 3 4	1 K K ² K ³	$A A \cdot k^{-1} A \cdot k^{-2} A \cdot k^{-3}$
i	K^{i-1}	$A \cdot k^{-i-1}$

elements appear whose size is k times smaller than the previous one. If d is the fractal dimension, then $K = k^{dn}$ (Frontier, 1994). If the SAD is also a fractal structure, during ecological succession and at each step of the succession, K times new species appear that are ktimes less abundant, which produced $K = k^d$ and d is a fractal dimension(Frontier, 1987, 1994, Mouillot et al., 2000). Thus, the relationship between the number of new species (N_i , starting from $N_1=1$, then $N_2=K$, $N_3=K^2$ and so on) and their respective relative abundance (F_i , starting from an arbitrary constant A, followed by A. k^{-1} , $A.k^{-2}$, $A.k^{-3}$, ...) at each step of the succession are listed in Table 1 (Frontier, 1987, 1994; Mouillot et al., 2000).

According to the mathematical derivation (Frontier, 1994),

$$F_r = F_0 \cdot (r + \beta)^{-\gamma} \tag{1}$$

This is the famous Zipf–Mandelbrot model in the SAD study. *r* is the rank (r=1, 2, 3, ... *S*); *S* is the species richness; *F_r* is the relative abundance of the *r*-th species sorted by its abundance; *F*₀ is the sum of all frequencies; γ =1/*d*, where *d* is the fractal dimension; and β =1/(*K*-1), where *K* is the multiple of the new species (Frontier, 1987, 1994; Mouillot et al., 2000). Frontier proposed that when β =0, the Zipf–Mandelbrot model can be transformed into the Zipf model ($F_r = F_0 \cdot r^{-\gamma}$) (Frontier, 1987, 1994).

However, in theory, $\beta \neq 0$ regardless of *K*. On the other hand, a larger *K* indicates that "these abundance distributions are made up of a series of plateaus as certain taxa exhibit the same abundance" (Mouillot et al., 2000), which is also impossible in actual community. Therefore, the Zipf–Mandelbrot model fails to include the Zipf model, and these two models are essentially different. It also fails to ensure that the rank must be an integer, because *K* is not always a whole number (Mouillot et al., 2000). In fact, *r* can only be an integer that increases in unitary increments rather than at a fixed multiplier (Frontier, 1987, 1994; Mouillot et al., 2000).

Accordingly, objectives of this study are to (1) constructs a SAD fractal model to ensure that r is an integer that increases in increments of 1 (see Section 2); (2) tests the SAD fractal model in the actual community (see Section 3); and (3) diversity index and SAD are based on the same information of community diversity (Tokeshi, 1993), but they are traditionally treated as separate themes with limited integration (Tokeshi, 2009). Therefore, this study will preliminarily integrate diversity index and SAD model into a broader perspective of community diversity (see Section 4).

2. Methods

According to the underlying fractal hypothesis (Frontier, 1987, 1994), species in a community are sorted by their abundance in descending order. To ensure that *r* was an integer, only one species was added at each step of the succession (Frontier, 1985, 1987, 1994; Mouillot et al., 2000). If one species was added after *r*, the rank was increased to r+1, and the multiple of the new species was $K_{r+1}=(r+1)/r$. If K_r times new species appeared that were k_r

Table 2

SAD fractal structure of present model. Ranking species abundance in descending order, the relationships of the rank (r), the multiple of new species (K_r) and abundance of the *r*-th species (N_r) at each step of ecological succession were shown.

Rank, r	the multiple of new species, K_r	Abundance of the r -th species, N_r
1	-	N ₁
2	2/1	$N_{1}(2)^{-1/d}$
3	3/2	$N_2 \cdot (3/2)^{-1/d}$
4	4/3	$N_3 \cdot (4/3)^{-1/d}$
r	r/(r-1)	$N_{r-1} \cdot [r/(r-1)]^{-1/d}$
•		

times less abundant, which produces $K_r = k_r^d$ (Frontier, 1985, 1987, 1994), $k_{r+1} = K_{r+1}^{1/d} = [(r+1)/r]^{1/d}$, and $N_{r+1} = N_r/k_{r+1} = N_r.[(r+1)/r]^{-1/d}$. Because r > 0, thus $k_{r+1} > 1$, and $N_r > N_{r+1}$. Then, the relationships of the rank (r, starting from r=1, then 2, 3, and so on), the multiple of new species (K_r) and abundance of the r-th species (N_r , starting from an arbitrary constant N_1 , followed by $N_1 \cdot k_2^{-1}$, $N_2 \cdot k_3^{-1}$, $N_3 \cdot k_4^{-1}$, ...) are listed in Table 2.

According to Table 2,

$$N_{2} = N_{1}(2)^{-1/d};$$

$$N_{3} = N_{2}(3/2)^{-1/d} = N_{1}(2)^{-1/d} \cdot (3/2)^{-1/d} = N_{1}(3)^{-1/d};$$

$$N_{4} = N_{3}(4/3)^{-1/d} = N_{1}(3)^{-1/d} \cdot (4/3)^{-1/d} = N_{1}(4)^{-1/d},$$
and analogously, $N_{r} = N_{1}r^{-1/d}.$

Let p = 1/d, then

$$\frac{N_r}{N_1} = r^{-p} \tag{2}$$

where *r* is the rank (r = 1, 2, 3, ..., S); *S* is the species richness; N_1 and N_r are the abundances of the 1st and *r*-th species by their abundance, respectively; $f_r (=N_r/N_1)$ is the relative abundance of the *r*-th species, and *d* is the fractal dimension. Let $y_r = \log f_r$ and $x_r = \log r$, the fitting procedure becomes:

$$y_r = -px_r \ (r = 1, \ 2, \ 3, \ \dots S)$$
 (3)

Thus, the best-fit value of p can be solved exactly by minimizing the sum of squared errors. The error to be minimized is:

$$\sum_{r=1}^{S} (-px_r - y_r)^2 \tag{4}$$

such that best estimate of p that minimizes this error can be found by taking the partial derivative of the error with respect to p and setting this equal to zero,

$$\sum_{r=1}^{5} 2(px_r + y_r)x_r = 0$$
(5)

Therefore, the best estimate *p* given the observations x_r (=log *r*) and y_r (=log f_r) is:

$$p = -\frac{\sum_{r=1}^{S} x_r y_r}{\sum_{r=1}^{S} x_r^2}$$
(6)

In figures, *p* is the slope with x_r on the abscissa and y_r on the ordinate, and the quality of fits can be measured by the goodness of fit (R^2), which denotes the goodness of fit on the log-transformed variables (log *r* and log f_r). R^2 is closer to 1, the result of fit is better.

To integrate the diversity index and the SAD model, the Shannon index (H) and the Simpson index (D) are introduced in this study.

H['] is one of the most enduring of all diversity indexes (Frontier 1987; Magurran, 2004), even though it has often been criticized

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