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Multifractal analysis of diversity scaling laws in a subtropical forest

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ABSTRACT

Understanding pattern of species diversity is a central goal of the science of ecology, and scaling laws are useful for revealing biodiversity patterns across scales. A transect along an altitudinal gradient in Dinghushan Reserve was used to test for the fractal effect in subtropical forest, and the multifractal method was used to validate the common scaling law of diversity. The results showed that: (1) richness-abundance pattern has self-similar relations (fractal effect) in the community despite a significant altitudinal gradient and habitat heterogeneity; (2) the power-law scaling relationship holds for all stratal levels of the forest (trees, shrubs and herbs), and hence scaling laws were significant; and, (3) the Shannon index was the optimal descriptor of tree species diversity information, but not shrub or herb diversity information in this subtropical forest. We also found that diversity indices that corresponding to $q > 1$ are descriptive of communities dominated by common species. In contrast, diversity indices that corresponding to $q < 1$ are suitable for communities with large numbers of rare species and high species evenness. The range of values of q for which scaling laws existed increased with the increasing latitude.

1. Introduction

The effect of scale on patterns of species diversity has long been of interest in ecology (Arrhenius, 1921; Bormann, 1953; Greig-Smith, 1952; Imagawa et al., 1966; Tillyard, 1914), and has been the focus of many studies over the past two decades (Dungan et al., 2002; Jelinski and Wu, 1996; Legendre and Fortin, 1989; Peterson and Parker, 1998; Turner et al., 1989; Wiens, 1989). This recent increase in attention has resulted from the increasing focus of biodiversity researchers on the mechanisms maintaining diversity.

Species are heterogeneously distributed across landscapes and are often organized within distinct communities (Gaston, 1994b, 2000) over several scales (Auerbach and Shmida, 1987; Lyons and Willig, 1999). Species diversity is usually measured for a given area (and, hence, scale), and thus depends on the sampling area. There are no simple and reliable rules to compare studies conducted at different scales (He et al., 2002). Therefore, developing a universal scaling law of biodiversity is one of the greatest challenges to ecologists (Hubbell, 2001). Such a law could be useful for understanding patterns of species richness, species extinction probabilities, species coexistence, resource-partitioning processes, and for reserve design (Gaston, 1994a).

As the area sampled increases in size, both species richness and abundance increase monotonously (Ye et al., 1998), and the number of species encountered is proportional to a power of the area sampled (SAR) (Macarthur and Wilson, 1967):

$$S(A) = cA^D$$

where $S(A)$ is species richness in a given area A; c is a constant; and D is the scaling exponent or fractal dimension (Li, 2000a). This power-law revealed to researchers the fractal nature of ecological communities, and is considered one of the few robust laws of ecology (Borda-de-Agua et al., 2002; Harte et al., 1999; Ostling et al., 2003, 2004). The power-law has been used to characterize community structure, estimate species richness, measure disturbance effects, determine the appropriate size of natural reserves in conservation biology (He and Legendre, 1996) and estimate species extinction rates (May et al., 1995; Pimm et al., 1995).

Species richness is one of the diversity metrics that can be related to each other using Rényi's generalized entropy function (Hill, 1973; Pielou, 1975; Rényi, 1970):

$$H_q = \frac{\log \sum_{i=1}^{s} p_i^q}{1 - q}$$

where q is an integer and p_i is the relative abundance. The logarithm of most classical diversity metrics are special cases of H_q.

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For example, the logarithm of species richness ($S(A)$), the Shannon and Inverse Simpson indices are H_q at $q = 0$, $q = 1$ and $q = 2$, respectively. Thus, the SAR can be generalized as follows:

$$\exp(H_q(A)) = C_q A^{D_q}$$

where $\exp(H_q(A))$ is the species richness (or other diversity index), C_q is a constant, and D_q is the scaling exponent or fractal dimension. A is the sample area. This function represents an ecological scaling law. If scaling relationships are examined over the range of q, then the analysis of the SAR becomes multifractal. When a fractal is observed, typically a more general class of self-similar relations called "multifractals" also exists (Mandelbrot and Evertsz, 1995). In contrast to a fractal object, or signal, where a single number or its "dimension" is sufficient for its complete characterization, characterization of a multifractal requires an infinite number of indices, frequently called "a spectrum". Multifractals are mainly probabilistic (Borda-de-Agua et al., 2002). Though fractal theory has existed for some time, multifractal analysis has seldom been applied to analyze cross-scale biodiversity patterns in subtropical forests.

In this study, a plant transect over an elevational gradient in the Dinghushan Mountains was used to test for the fractal effect in a subtropical forest, and a multifractal method was used to validate the common scaling law of diversity. The study objectives were to: (1) test whether or not the power law exists in the biodiversity patterns of subtropical forest; (2) test whether or not fractal effects can be found across several spatial scales; and (3) determine a criterion for choosing the optimal diversity index for different forest communities. Various factors that may influence the significance of the scaling law were also examined, in order to find the relationship between latitude and the values of q for which the scaling law is significant. This analysis contributes to our understanding of how species are distributed, and also how species diversity in subtropical forests.

2. Methods

2.1. Study area

The study site was located in the Dinghushan Mountains (112°30′39″–112°33′41″E, 23°09′21″–23°11′30″N) in Guangdong Province. Dinghushan was the first Nature Reserve established in China (in 1956), and it has played a significant role in the conservation of forest ecosystems over the past 50 years. The reserve comprises low mountains and hilly landscapes. Its total area is 1155 ha, with an elevational range of 14.1–1000.3 m (above sea level), and it is composed of tropical-subtropical forest. Dinghushan has a southern subtropical monsoon climate with a mean annual temperature of 20.9 °C, and mean monthly temperatures of 12.6 °C in January and 28.0 °C in July. Average annual precipitation is 1929 mm, with most precipitation occurring between April and September. Annual evaporation is 1115 mm and relative humidity 82 percent.

2.2. Sampling methods

A 10 × 1160 m transect was established from the foot to the top of Sanbaofeng hill in Dinghushan in 2003. The transect covered an altitudinal range from 50.2 m to 476.5 m, and included monsoon evergreen broad-leaf forest, coniferous and broad-leaf mixed forest. The transect was subdivided into 232.5 m × 10 m quadrats for convenience in taking field surveys. The survey consisted of enumerating all free standing trees and shrubs at least 1 cm in diameter at breast height (DBH), locating each tree using geographic coordinates on a reference map, and identifying it to species. Within each quadrat, a 2 m × 5 m sub-quadrats was selected to survey shrubs and herbs. For the shrubs, individuals with a DBH of less than 1.0 cm were counted, their heights measured, and they were identified to species. The percent cover of each species was also estimated. For the herbs, the percent cover, individual heights, and number of individuals were recorded for each herbaceous species. Treat tree layer, shrub layer, and herb layer separately in order to be able to compare our results to those of other studies, some of which only worked with trees species.

2.3. Multifractal analysis

2.3.1. Theoretical background

In multifractal analysis, Rényi dimensions (Hentschel and Procaccia, 1983; Rényi, 1970) are defined as:

$$D_q = \frac{\lim_{\delta \to 0} \log[\sum_{i=1}^{n(\delta)} u_i(\delta)^q]}{(q-1)\log(\delta)} \tag{1}$$

where q is any real integer other than 1. When $q = 1$, D_q becomes (Loehle and Li, 1996):

$$D_1 = \frac{\lim_{\delta \to 0} \sum_{i=1}^{n(\delta)} [u_i(\delta)\log(u_i(\delta))]}{\log(\delta)} \tag{2}$$

D_1 is called the *entropy dimension* or *information dimension* of the distribution (Hentschel and Procaccia, 1983; Rényi, 1970), and it quantifies the rate of growth of entropy with respect to δ. This expression can be considered as a u-weighted average of the singularity strength values. It is also related to the size (dimensions) of the minimal set, where the whole measure is concentrated (Evertsz and Mandelbrot, 1992). The dimension D_0 is called the *capacity dimension* and D_2 is the *correlation dimension* (Peitgen et al., 2004). The greater the variation of D_q with respect to q, the higher the degree of heterogeneity of the measure. When an adequate scaling behavior takes place for an experimental measure, the spectrum of Rényi dimensions, D_q, provides a valuable characterization of the singular behavior of the measure and the respective interpretation within each context (Harte, 2001).

Taking the negative of the numerator of Eq. (2) gives (Jumarie, 2000; Li, 2000a):

$$H(\delta) = -\sum_{i=1}^{n(\delta)} [u_i(\delta)\log(u_i(\delta))] \tag{3}$$

This is the Shannon entropy (Loehle and Li, 1996; Shannon and Weaver, 1948), a measure of the heterogeneity or unevenness of a forest community. $u_i(\delta)$ is the probability of observing a species in the ith cell using samples of δ units in size (Chen et al., 2005)

2.3.2. Rényi dimensions calculation

For the sampling transect data, the original quadrat data were pooled to create tree, shrub and herb data sets for samples of different areas (called "cell size"), δ: 10 × 10, 20 × 10, 40 × 10, 145 × 10, 290 × 10, 580 × 10 and 1160 × 10 m. Hence, there were a total of 116, 58, 29, 8, 4, 2 and 1 replicate(s) or cell(s) ($n(\delta)$), for each sample area listed above, respectively. Thus, species j in cell i of cell size δ has a relative abundance value of $u_{ij}(\delta)$ ($j = 1, 2, 3, \ldots N_i$, where N_i was the number of species in cell i).The relative abundance $u_{ij}(\delta)$ is defined as(Alatalo, 1981):

$$\mu_i(\delta) = \frac{h_i(\delta)}{3th_i} + \frac{c_{ij}(\delta)}{3tc_i} + \frac{a_{ij}(\delta)}{3ta_i} \tag{4}$$

where $h_{ij}(\delta)$, $c_{ij}(\delta)$ and $a_{ij}(\delta)$ are the sum of the height, percent cover and abundance of species j in cell I, with cell size δ(scale); th_i, tc_i,