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## Multifractal analysis of neutral community spatial structure

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## HIGHLIGHTS

- The spatial organization of neutral communities possesses a multifractal structure.
- The curves of area-dependence of SAD moments demonstrate almost perfect scaling collapse with respect to the dispersal distance.
- Multifractal spectra reveal patterns of dominance and rarity and its dependence on the speciation rate and dispersal kernel.
- Communities with the same SAR exponent may possess differences in scaling of dominance and rarity.
- Negative dimensions in spectra reflect the pattern of scaling of singletons' richness.

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## ABSTRACT

The spatial structure of neutral communities has nontrivial properties, which are described traditionally by the Species–area relationship (SAR) and the Species Abundance Distribution, (SAD). Fractal analysis is an alternative way to describe community structure, the final product of which – a multifractal spectrum – combines information both on the scaling parameters of species richness (similar to SAR), and about species' relative abundances (similar to SAD). We conducted a multifractal analysis of community spatial structure in a neutral lattice-based model.

In a realistic range of dispersal distances, moments of the species abundance distribution form a family of curves of the same shape, which are reduced to a single universal curve through a scaling collapse procedure. Trivial scaling is observed on small and large scales, which reflects homogeneity of species distribution at small scales and a limiting log-series distribution at large scales. Multifractal spectra for different speciation rates and dispersal kernels are obtained for the intermediate region of scaling. Analysis of spectra reveals that the key model parameters determine not only the species richness and its scaling, but also of species dominance and rarity. We discovered a phenomenon of negative dimensions in the multifractal spectrum. Negative dimensions have no direct interpretation from a purely physical point of view, but have biological meaning because they reflect the negative relationship between the number of singletons and the area.

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## 1. Introduction

Development of the unified neutral theory of biodiversity and biogeography is regarded as one of the major achievements of theoretical ecology of the last decade (Hubbell, 2001; Alonso et al., 2006; Rosindell et al., 2011). Although the basic assumptions underlying neutral models (ecological equivalence of individuals, simplified mechanisms of speciation) are obviously unrealistic (Clark, 2009), neutral theory gives a structural framework for

understanding the fundamental processes governing the mechanics of community functioning, such as dispersal limitation.

Most of the existing neutral models ignore community spatial structure and model it implicitly with two separate spatial scales: a local community and a metacommunity (Hubbell, 2001; Volkov et al., 2003). Local and global communities in such models are connected in a one-way direction by immigration and undergo separate dynamics. The attractiveness of implicit space modeling is that you can get exact analytical solutions (Volkov et al., 2003; McKane et al., 2000) and construct a sampling theory that permits model parameterization on the basis of empirical data (Alonso and McKane, 2004; Etienne, 2005; Etienne, 2007; Etienne and Alonso, 2005).

Neutral models with explicit space in which individuals have exact spatial location are less common. In this case potential of

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interaction between individuals is more or less limited by distance. Most spatial neutral models are based on a 2-dimensional lattice (Durrett and Levin, 1996; Chave et al., 2002; Rosindell and Cornell, 2007; Rosindell and Cornell, 2009; Rosindell and Cornell, 2013; Pigolotti and Cencini, 2009; Horvát et al., 2010; Cencini et al., 2012; Derzsi and Nédá, 2012). Individuals occupy lattice cells and the space thus has a discrete nature. First attempts to study spatial structure of neutral models with continuous space appeared recently (Grilli et al., 2012; O'Dwyer and Green, 2010). However these considerations start in a similar manner from discrete lattice and then make a limit transition to continuity.

In the study of community spatial structure, focus has traditionally been paid to the species–area relationship (SAR), often regarded as one of the few law-like generalizations in ecology (Lawton, 1999; Lomolino, 2000). The most widespread form of the SAR is the power function. Its history goes back to the “Darwinian” 1859 year and the work of Watson (Rosenzweig, 1995). The main parameter of the SAR is its slope in bilogarithmic coordinates  $z$ , describing the rate of accumulation of species richness. The higher the value of  $z$ , the faster species richness grows with increasing area. Theoretical limits for  $z$  are 0 (fixed species richness) and 1 (simple linear proportionality). It was shown (Harte et al., 1999; Harte et al., 2001) that the power-law SAR is equivalent to a self-similar distribution of species richness. In this context, the slope  $z$  can be interpreted as corresponding to fractal dimension.

For neutral lattice models it has been found that a typical SAR has a triphasic structure: at very small and very large scales it has a unit slope (species richness is directly proportional to area), while intermediate scales show the power-law dependence (Rosindell and Cornell, 2007; Rosindell and Cornell, 2009). The slope  $z$  of the intermediate phase is determined by the rate of speciation  $\nu$  (probability of mutation into new species). Reduction of  $\nu$  leads to a general decrease in species richness and slope  $z$  decreases approximately as  $z \propto -1/\log \nu$  (Pigolotti and Cencini, 2009).

Species richness at a particular scale is a very general descriptor of community structure. It does not take into account the ratio of species abundances and species relative roles in the local dynamics. Thus, the SAR is only a first approximation to the description of community spatial structure. For a more complete understanding we need to introduce new measures that take into account not only the presence of different species at some location, but also their relative abundances. The classical approach here is the study of the Species Abundance Distribution (SAD). Within the framework of neutral theory, SADs are well studied for models with implicit space, but a strict correspondence between parameters of spatial and non-spatial models is missing (Chisholm and Lichstein, 2009; Etienne and Rosindell, 2011). In a recent paper Rosindell and Cornell (2013) conducted a direct analysis of SAD in the lattice model by computer simulation. They demonstrated that increasing of scale leads to the systematic changes in SAD from the left-hand asymmetric form with predominance of rare species to unimodal (log-normal-like) and bimodal forms to the limiting case of a log-series at extremely large scales. It was also shown that in general, the SAD depends on a complex parameter, which is a combination of area, speciation rate and average dispersal distance.

The approach of Rosindell and Cornell (2013) was based on the consideration of SADs, obtained at the different spatial scales. Here we propose to use a different approach to study the spatial structure of neutral communities, based on a multifractal analysis (Harte, 2001; Borda-de-Água et al., 2002; Iudin et al., 2003). With this approach, the community is considered as a fractal set consisting of a range of subsets of species with different abundances (full spectrum from strong dominants to extremely rare species). Fractal dimensions of these subsets (which are descriptors of

species richness) are determined by investigation of scaling of species distribution moments. As a measure of scale it is possible to use area (Borda-de-Água et al., 2002) as well as other measures of sampling effort (Iudin et al., 2003). Multifractal analysis of the structure of biological communities has now been applied to terrestrial (Borda-de-Água et al., 2002; Zhang et al., 2006; Gelashvily et al., 2008; Gelashvili et al., 2010; Yakimov et al., 2008) and aquatic communities (Iudin et al., 2003; Gelashvili et al., 2012) and has established itself as a promising method for analyzing multiscale phenomena.

In this paper, we apply multifractal analysis to the study of spatial structure of the neutral lattice model of Rosindell and Cornell (2007, 2009). Results of multifractal analysis at small and large scales are trivial and reflect homogeneity of species distribution at small scales and a limiting log-series distribution at large scales. For intermediate scales we have got multifractal spectra describing patterns of dominance and rarity in the community. The interpretation of spectra is in many respects analogous to traditional SAR slope  $z$ . At the same time the spectrum discloses information about scaling of the total species richness (folded in the exponent  $z$ ) to a continuum of indicators describing the scaling of the richness in groups of species, which have different abundance. That is why the analysis of dependence of spectra shape on speciation rate and dispersal kernels gives a deeper understanding of spatial structure of the community in comparison with analysis of the SAR.

We consider the presence of the complex form of spatial scaling in a relatively simple neutral model as a manifestation of self-organized criticality (SOC). SOC is a property of dynamical systems that evolve spontaneously to the critical state. Their spatio-temporal dynamics in critical state display self-similarity. In this context, neutral communities belong to a broad class of nonlinear self-organizing systems with critical behavior, which in this case is manifested in the fact that any species has a chance to take a dominant position.

## 2. Methods

### 2.1. Neutral community model

A spatially explicit neutral community model (Rosindell and Cornell, 2007) describes a community of sessile organisms (for example, trees in a forest or macrobenthos). At the core of the simulated community is a lattice with each cell containing a single individual, which does not move during its lifetime. The dynamics of the model are governed by processes of individual death, reproduction (linked to dispersal) and speciation. A randomly chosen individual dies at each simulation step. Because of saturation of ecological space the vacant place is filled immediately: an offspring of another individual remaining on the lattice occupies the empty cell. The choice of parent individual is random according to the dispersal kernel  $K(r)$ . Mutation may occur during reproduction with probability  $\nu$  and then new individual gives rise to a new species (speciation by point mutation).

Thus, the key parameters of the model are speciation rate  $\nu$  and the form and scale  $L$  of the dispersal kernel. In this paper, we use the following dispersal kernels defining the density of the probability that the distance between an ancestor and a descendant equals  $r$ :

$$\text{Normal distribution : } K(r) = \frac{1}{L\sqrt{2\pi}} e^{(-r^2/2L^2)}, \quad (1)$$

$$\text{Exponential distribution : } K(r) = \frac{1}{2L} e^{(-r/L)}, \quad (2)$$

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