

## Phylogenetic Diversity Scaling in Small Mammal Communities: The Example of Nizhny Novgorod Region of the Volga Basin

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**Abstract**—Traditional approaches to structural analysis of biotic communities, based on the data on species abundances, do not take into account phylogenetic relationships between these species. We propose a new approach to studying the scaling (scale dependence) of phylogenetic diversity by means of multifractal analysis in which the moments of phylogenetic diversity are used. The results of applying this approach to small mammal communities of Nizhny Novgorod region of the Volga Basin has shown that phylogenetic diversity scaling complies with the power law, which is indicative of the self-similarity of these communities. The multifractal spectra of phylogenetic diversity scaling markedly differ from the spectra of species diversity scaling, providing evidence that the proposed approach can provide novel information on the structure of biotic communities.

**Keywords:** community structure, phylogenetic diversity, multifractal analysis, scaling

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Traditional approaches to studies on the structure of communities and their diversity are based on analyzing species composition and representation (relative abundance) of species in the samples and using the results to calculate various indices of diversity and similarity [1, 2], with the constituent species being regarded as independent and equidistant structural units. From the biological standpoint, this is a significant simplification of the real situation. The species have evolutionary history and a system of kinship relationships, and, with all other conditions being equal, a community of closely related species (e.g., the marten, sable, and weasel) is characterized by lower diversity than a community consisting of unrelated species (e.g., the marten, vole, and deer).

The degree of kinship between the species comprising a community is evaluated on the basis of information contained in their phylogenetic tree. Due to recent advances in molecular systematics and phylogeny, such studies on many taxonomic groups have become feasible in recent years. A series of indices of phylogenetic diversity and similarity have been proposed that allow evolutionary history to be taken into account in analyzing the community structure [3, 4]. They are calculated based on the data on species composition and relative abundance in the samples and on the phylogenetic tree (its hierarchy and branch lengths). As in the case of measuring species similarity and diversity, qualitative and quantitative indices of

phylogenetic similarity and diversity are available that take or do not take into account the relative abundances of species. The simplest of them is Faith's index *PD* [5] calculated as the sum of branch lengths in the tree constructed for all species in a given sample. This index (an analog of species richness) reflects the length of evolutionary history in a given set of species.

Almost all parameters of populations, communities, and ecosystems depend on the scale at which they are measured. The problem of scale dependence of certain parameters (a particular form of such a dependence is here referred to as scaling) has been attracting special attention from ecologists during the past few decades [6–8]. The positive scale dependence of diversity has been well studied. A direct way to evaluate diversity scaling is to analyze the species accumulation curves and the species–area relationships. In both cases, the power law is regarded as a classical mathematical model for the dependence of the number of species on the scale. Hence, the question has arisen concerning fractality in the community structure [9–11], since the power function is characterized by scale invariance. Based on the concept of community self-similarity, the method involving multifractal analysis has been proposed for describing community structure [11–14].

Research on the scale dependence of species diversity has more than 150-year history, whereas the scale dependence of phylogenetic diversity is poorly stud-

ied, and available publications deal only with qualitative indices [15–18].

Here we propose a new approach to the study of phylogenetic diversity scaling by means of multifractal analysis applied to the moments of phylogenetic diversity, i.e., the normalized sum of branch lengths in a phylogenetic tree for all species found in a given sample. The fractal analysis of phylogenetic diversity scaling makes it possible to describe the community structure by a multifractal spectrum that comprises information on the relative abundances and phylogenetic diversity of constituent species.

The procedure and results of this analysis are largely similar to those of multifractal analysis of species diversity scaling, which we have developed previously. Here, this method is applied to two small mammal communities of the Nizhny Novgorod region of the Volga Basin, which have already been successfully studied using the traditional approach [19].

### MATERIAL AND METHODS

Small mammals were studied in two natural geographic zones of Nizhny Novgorod region separated by the Volga river: the forested left-bank area and forest–steppe right-bank area. The census of rodents and insectivores was taken by conventional methods [20] in 2005 and 2006. On the whole, 67 quantitative samples were taken, which contained 20 small mammal species. The initial data set was described in detail [11, 19].

The analysis of phylogenetic diversity is based on a dated phylogenetic tree comprising all the species represented in the community studied. In an ideal case, this tree is dated and dichotomic, i.e., the branch lengths are measured in million years since the moment of divergence (or in the number of base substitutions per locus) and the tree itself has no polytomies (nodes with more than two descendant lineages).

The phylogenetic supertree of 4510 species of the class Mammalia was constructed and published in 2007 by an international research team [21] and has since found wide application in studies on the phylogeny of mammals. We used it as a source of phylogenetic data to analyze small mammal communities of Nizhny Novgorod region. As noted above, samples from two zones contained 20 Insectivora and Rodentia species, with all of them being represented in the supertree of mammals. For our purposes, we constructed a phylogenetic tree for only these 20 species, which contained four polytomies (Fig. 1).

The fractal analysis of diversity scaling is based on evaluating the scale dependence of the moments of diversity. Different parameters may serve as a measure of scale, including the area, sampling effort, and the total number of individuals [11]. In our case, the total number of trap–days expended to collect the samples was used as such a measure.

To analyze scaling, we propose to use the moments of phylogenetic diversity ( $PM_q$ ), which are determined by summing up all weighted branch lengths in the phylogenetic tree comprising all species found in a given sample:

$$PM_q = \sum_{i=1}^b L_i \left[ \frac{a_i}{T} \right]^q, \tag{1}$$

where  $b$  is the number of branches,  $L_i$  is the length of the  $i$ th branch,  $a_i$  is abundance of the  $i$ th branch determined as the sum of relative abundances of all species descending from this branch,  $T$  is the depth of the tree (the distance from the root to the top), and  $q$  is the order of the moment.

The moments of phylogenetic diversity defined as above are related to the parametric family of phylogenetic diversity indices  ${}^qPD$  proposed by Chao et al. [22, 23]:

$${}^qPD = PM_q^{1/(1-q)}. \tag{2}$$

The same relationship exists between the moments of species diversity and number equivalents of Rényi entropies.

The zero-order moment of phylogenetic diversity is as follows:

$$PM_0 = \sum_{i=1}^b L_i \left[ \frac{a_i}{T} \right]^0 = \sum_{i=1}^b L_i = PD, \tag{3}$$

i.e., this is the Faith index (the total length of evolutionary history), an analog of species richness in the analysis of phylogenetic diversity. The first-order moment of phylogenetic diversity is equal to unity:

$$PM_1 = \sum_{i=1}^b L_i \frac{a_i}{T} = \frac{\sum_{i=1}^b L_i a_i}{T} = \frac{T}{T} = 1. \tag{4}$$

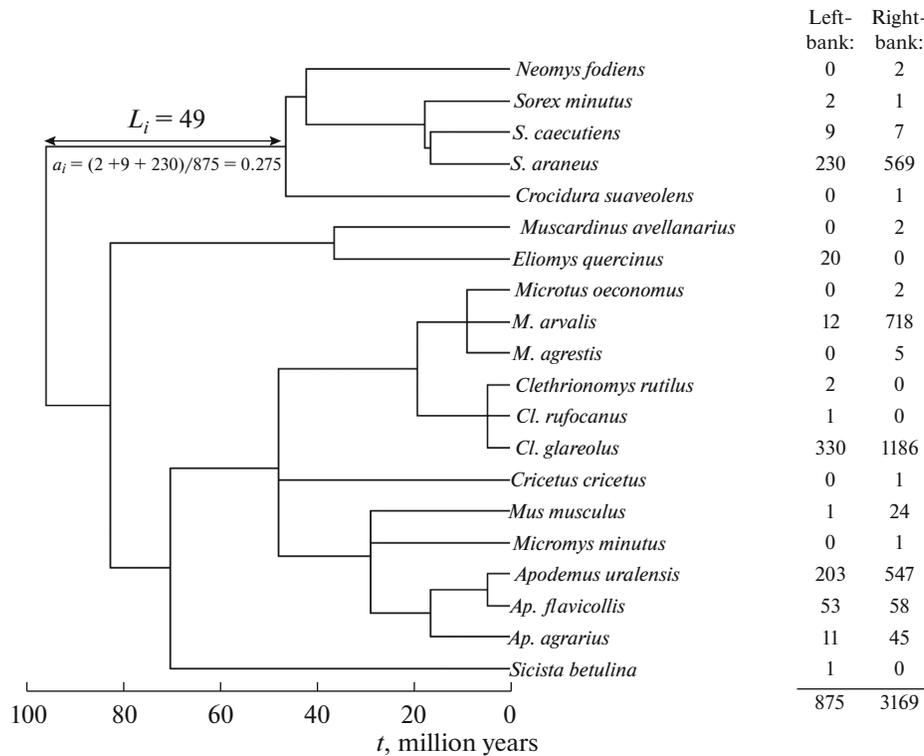
The third parity is based on the fact that the total length of branches (weighted by their abundances) is equal to the tree depth [22]. It can be shown that the second-order moment of phylogenetic diversity is related to Rao’s quadratic entropy  $Q$  [24]:

$$PM_2 = \sum_{i=1}^b L_i \left[ \frac{a_i}{T} \right]^2 = \frac{1-Q/T}{T}. \tag{5}$$

A community is regarded as a fractal object if the phylogenetic diversity moments of all orders in this community comply with the power-law scaling:

$$PM_q(N) \propto N^{\tau(q)}, \tag{6}$$

where  $N$  is the measure of scale and  $\tau(q)$  are mass exponents. In forming  $PM_q(N)$  dependencies, different schemes of combining samples into groups (sets) can be used. In particular, we used a hierarchical scheme when analyzing small mammal communities: individual samples → clusters of samples from geo-



**Fig. 1.** Phylogenetic tree for 20 species found in small mammal communities of Nizhny Novgorod region. Table on the right shows total numbers of animals in all samples from the two geographic zones. The branch comprising Insectivora species is supplied with data on its length ( $L_i$ ) and abundance ( $a_i$ ) calculated for the total sample from the left-bank community.

graphically close sites  $\rightarrow$  total (pooled) sample (for details, see [19]). Since the power law (Eq. (6)) in double logarithmic coordinates corresponds to linear dependence, the conformity of the empirical scaling of the moments to the power law was checked using the curvilinearity test and Akaike information criterion (comparison of linear and quadratic approximations).

If the scaling of the moments complies with the power law and, hence, the community displays self-similarity, it can be described by the multifractal spectrum, which is obtained by applying the Legendre transform to the spectrum of mass exponents  $\tau(q)$ :

$$\begin{cases} a(q) = -\frac{d}{dq} \tau(q) \\ f(a(q)) = qa(q) + \tau(q) \end{cases} \quad (7)$$

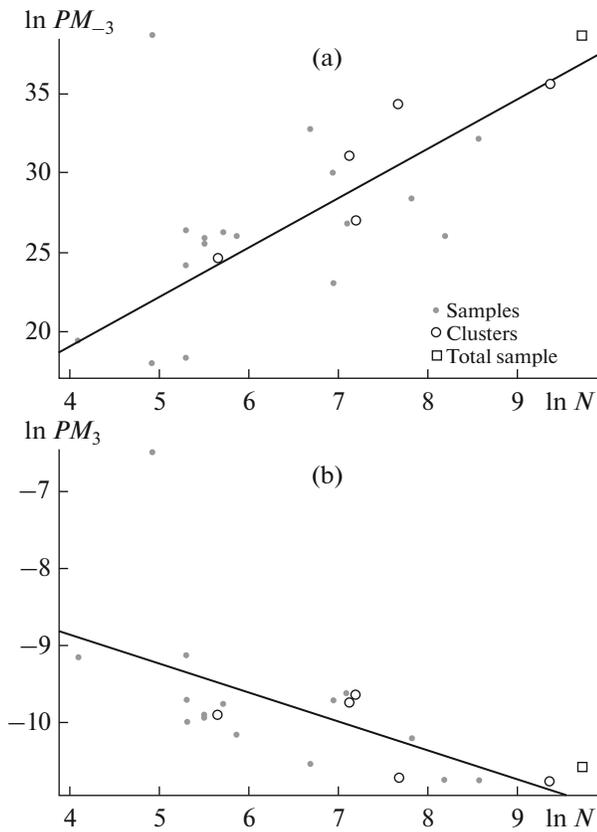
The mass exponents themselves are estimated empirically based on Eq. (6), and singularity indices  $a(q)$  in the first equality of Eq. (7) are estimated by numerical differentiation methods.

The interpretation of the multifractal spectrum of phylogenetic diversity scaling is generally similar to that of the multifractal spectrum of species diversity scaling. A community whose structure is analyzed using multifractal analysis is considered as a set that consists of subsets comprising species differing in abundance, from dominants to rare species. The sin-

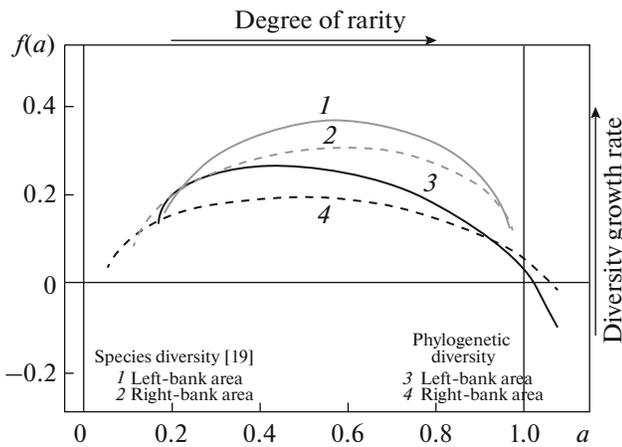
gularity index  $a$  (the abscissa of the spectrum plot) characterizes species rarity: the higher the index, the more rare the species. Species richness is the “natural” measure of species diversity in the subsets, and the length of evolutionary history  $PD$  is the corresponding measure of phylogenetic diversity. The fractal dimension  $f$  (the ordinate of the plot) in the common spectrum characterizes the rate of increase in species richness in groups of species with different abundances. Correspondingly, this dimension in analysis of phylogenetic diversity is interpreted as the rate of increase in the sum of branch lengths (the length of evolutionary history) in the tree that combines all species in the groups depending on species abundance. Thus, the spectrum represents the structure of the community in the axes of “rarity” and “rate of change in diversity.” The top of the spectrum characterizes the scaling of the complete evolutionary history of the community, and its left and right branches characterizes the scaling of evolutionary history for the groups of species with high or low abundance.

## RESULTS

Analyzing phylogenetic diversity scaling in small mammal communities of Nizhny Novgorod region, we regarded left- and right-bank areas as separate experimental units. The moments of phylogenetic



**Fig. 2.** Plots of scale dependence for the moments of phylogenetic diversity (a)  $PM_{-3}$  and (b)  $PM_3$  in the small mammal community of left-bank area in double logarithmic coordinates;  $N$  is the measure of scale (number of trap-days).



**Fig. 3.** Multifractal spectra of species and phylogenetic diversity scaling for small mammal communities of Nizhny Novgorod region.

diversity  $PM_q$  were calculated for the orders of  $-3$  to  $+3$  with a step of  $0.1$  for each set of samples, including the initial ones. Figure 2 shows the plots of scale dependence for the moments  $PM_{-3}$  and  $PM_3$  in the left-bank community. The moments of orders  $q < 1$

increase with scaling-up, while those of orders  $q > 1$  decrease. The plots have the form of a cloud of points, with this scattering around the trend line increasing with an increase in the order of the moment. The same tendencies are characteristic of the scaling of species diversity moments [11].

The scaling of phylogenetic diversity moments in both communities was analyzed for compliance with the power law (Eq. (6)). No deviations were revealed: for the moments of all orders ( $q$ ), the coefficient at the quadratic term did not differ significantly from zero according to the curvilinearity test, and the value of Akaike information criterion for linear approximation in double logarithmic coordinates proved to be minimal. Thus, small mammal communities of Nizhny Novgorod region could be considered self-similar with respect to phylogenetic diversity scaling and, therefore, appropriate for multifractal analysis.

The spectrum of mass exponents  $\tau(q)$  was evaluated from the slope estimates of linear regression of the moments versus scale in double logarithmic coordinates. The regression lines are shown in Fig. 2 along with the cloud of points corresponding to empirical data. Figure 3 shows multifractal spectra describing phylogenetic diversity scaling in small mammal communities of Nizhny Novgorod region and, for comparison, the multifractal spectra of species diversity scaling obtained in our previous study [19].

The rate of increase in Faith's index (reflecting the total length of evolutionary history) is higher in the left-bank community: the top of the spectrum for this community lies above the apex of the spectrum for the right-bank community. The level of dominance in the left-bank community is lower, whereas the rate of increase in the length of evolutionary history in the group of abundant species is higher than in the right-bank community: the left (ascending) branch of the right-bank community spectrum lies below and on the left of this branch in the left-bank community spectrum. The situation for rare species is inverse, and the rate of increase in the length of evolutionary history is higher in the right-bank community: the right, descending branches of the spectra cross each other, with the extreme right part of the right-bank community spectrum lying higher.

Thus, the results of comparative analysis of the multifractal spectra of phylogenetic diversity scaling in two small mammal communities of Nizhny Novgorod region are generally similar to the results of analysis of multifractal spectra obtained without taking into account phylogenetic data [19], but all tendencies noted above are manifested more clearly. A new phenomenon (not characteristic of common multifractal spectra) is that the right, descending branches of the spectra extend beyond the unity line on the abscissa and to negative values on the ordinate. The latter means that diversity (the length of evolutionary history) in the group of rare species decreases rather than

increases [25]. This effect could not be revealed without taking into account phylogenetic data. The singularity index in excess of unity is evidence that the minimum representation (abundance) associated with the branches of phylogenetic tree decreases with scaling-up at a higher rate than does inverse proportionality. This phenomenon is not characteristic of multifractal spectra of species diversity and needs more detailed analysis.

## DISCUSSION

In this study, we have developed and tested a new version of multifractal analysis for describing phylogenetic diversity scaling in biotic communities. New parameters such as the moments of phylogenetic diversity have been proposed to integrate phylogenetic data into multifractal analysis. It is shown that the moments of phylogenetic diversity of different orders are connected with other indices of phylogenetic diversity used in the ecological literature. The new variant of multifractal analysis is an amendment to the methods developed previously [11, 14, 25, 26]. It allows integration of additional data describing the system of phylogenetic relationships between the constituent species of the community under study. The final product of analysis—the multifractal spectrum of phylogenetic diversity scaling—can be regarded as a refined version of the conventional multifractal spectrum.

A multifractal analysis of phylogenetic diversity scaling in two small mammal communities of Nizhny Novgorod region has shown that the moments of phylogenetic diversity behave qualitatively similar to the moments of taxonomic diversity: the moments of orders  $q < 1$  increase, while those of orders  $q > 1$  decrease with scaling-up, with the pattern of change following the power law. A comparative analysis of the multifractal spectra of phylogenetic diversity scaling showed good correspondence with the results obtained with conventional multifractal spectra. However, all tendencies manifest themselves more clearly in the former spectra, and their analysis has made it possible to reveal the phenomenon of scale-up-dependent decrease of diversity in the group of rare species.

Thus, the results of testing the new variant of analysis confirm its adequacy and applicability. They do not contradict previous conclusions (which is additional evidence that the method is adequate to the purpose), and the fact that changes in multifractal spectra are better manifested when analyzing phylogenetic diversity indicates that the new variant of analysis has a high potential for discriminating between communities. This is not surprising, since additional data contained in the phylogenetic tree are used in this variant.

The proposed integration of phylogenetic data into the multifractal analysis of community structure is in line with the new generalizing approach that deals with three facets of biodiversity and community struc-

ture: taxonomic, phylogenetic, and functional [4, 27–29]. The taxonomic facet is basic, it corresponds to the traditional, historically developed approach to the analysis of species diversity. The two other facets take into account interrelations between species. The phylogenetic facet makes use of data on the structure of kinship relationships between species that are presented as a phylogenetic tree [30, 31], a taxonomic classification tree [32], or a matrix of genetic distances calculated from molecular genetic data [29]. The functional facet concerns data on the so-called functional traits, which are usually understood as species-specific traits directly or indirectly determining the fitness of individuals [33, 34]. This study presents the method for studying the scaling (scale dependence) of the phylogenetic facet of diversity. Likewise, data on the functional traits can be integrated into the multifractal analysis of community structure.

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