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Original article

Estimating the niche preemption parameter of the geometric series

Fangliang He[a,*], *Danling Tang*[b]

[a]*Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada*
[b]*LED, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou, China*

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ABSTRACT

The geometric series of niche preemption is one of the two major niche-based species-abundance models. Here a new, simple method was proposed to estimate the resource fraction parameter of the model. The performance of this method was compared with another two more complicated methods using four data of species-abundance from mixed-wood boreal forest, insect and fungus communities.

Niche theory assumes that niche differentiation is prerequisite for species coexistence (Hutchinson, 1959; Tilman, 1985). Each species is unique in its ability to utilize and compete for limiting resources, which determines the relative distribution of species-abundances in a community. The geometric series (also called niche preemption model) and MacArthur's broken stick model are the two major niche-based species-abundance models (Pielou, 1975; Fattorini, 2005). Opposite to the broken stick model, the geometric series describes communities of highly uneven species-abundance distribution and low diversity characterized by a few dominant species. Such communities are expected to arise from the mechanism of niche preemption by which a sequential colonization of species into a community is assumed. The first species that colonizes the community preempts the first k fraction of the total resource or space. The second species takes the k fraction of the remainder, and this partitioning process goes on until the filling of the entire niche space. Suppose that the abundance of each species is proportional to the niche they occupy, the abundances of the species in the community ordered from the most abundant to the least abundant are:

$$ck, ck(1-k), ck(1-k)^2, \ldots, ck(1-k)^{S-1},$$

where c is a constant that converts resource to abundance, S is the total number of species. Because the abundances summed over all the species must equal the community size N, $c = N/[1-(1-k)^S]$. The abundances of the S species thus form a geometric series:

$$n_i = \frac{Nk(1-k)^{i-1}}{1-(1-k)^S}, \quad i = 1, 2, \ldots, S. \tag{1}$$

The geometric series was first proposed by Motomura (1932) and has been widely used to describe communities of early succession (Whittaker, 1972; Bazzaz, 1975), disturbances (Gray, 1981; Nummelin, 1998; but see Nummelin and Kaitala, 2004) and poor habitats (Whittaker, 1965; Keeley and Fotheringham, 2003). It has recently also been shown that the model is intimately related to the Berger–Parker diversity index and

* *Corresponding author.*
E-mail address: fhe@ualberta.ca (F. He).
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useful for indicating the effects of disturbances on ecosystems (Caruso et al., 2006). A thorough treatment of the geometric series is given by May (1975) who also develops a method for estimating the niche preemption parameter k, which has become a standard method for estimating k (Magurran, 1988):

$$\frac{n_{min}}{N} = \frac{k(1-k)^{S-1}}{1-(1-k)^{S}}, \qquad (2)$$

where n_{min} is the abundance of the least abundant species. Numerical method (e.g., Newton's method) is needed to solve for k from Eq. (2).

Taking advantage of the fact that species-dominance curve of the geometric series is a simple line, Fattorini (2005) and Caruso and Migliorini (2006) use regression methods to fit the dominance curve. The regression takes the form of $\log(n_i) = a + \log(1-k)i$, where i is species rank, a and $\log(1-k)$ are regression coefficients.

Here we offer a third, but very simple, estimation method which takes account abundances of all species. The new method is:

$$k = 1 - \left(\frac{n_{min}}{n_{max}}\right)^{\frac{1}{S-1}}. \qquad (3)$$

Although only the abundances of the least and the most abundant species, n_{min} and n_{max}, appear in the formula, its derivation uses the abundances of all species. From Eq. (1) we have the ratio, $n_{i-1}/n_i = 1/1-k$. It is obvious that $(n_{max}/n_2)(n_2/n_3)\ldots(n_{S-1}/n_{min}) = (1-k)^{1-S}$. This leads to Eq. (3).

We now apply the new method to fit four empirical data and compare its performance against May's method (Eq. (2)) and the regression method. The first data set is tree species from a mixedwood boreal forest in northern Alberta, Canada (Fig. 1a). In the summer of 2006 we established 1 ha (100 × 100 m) tree plot. Trees with diameter at breast height equal to or larger than 1 cm were mapped, enumerated and identified to species. There are six tree species with a total of 1614 stems. The least abundant species is Balsam poplar (*Populus trichocarpa*) with abundance = 2 and the most abundant species is Balsam fir (*Abies balsamea*) with abundance = 1076. The k estimated from Eq. (3) is 0.71566; its estimate from Eq. (2) is 0.72001, while it is 0.72277 from the regression method.

The second data are from Niemelä et al. (2002) that is Carabid beetle species collected from a rural forest near Edmonton, Alberta, dominated by trembling aspen (*Populus tremuloides*) (Fig. 1b). There are 29 species and 1308 individuals. The most abundant beetle has 328 individuals. The k estimated from

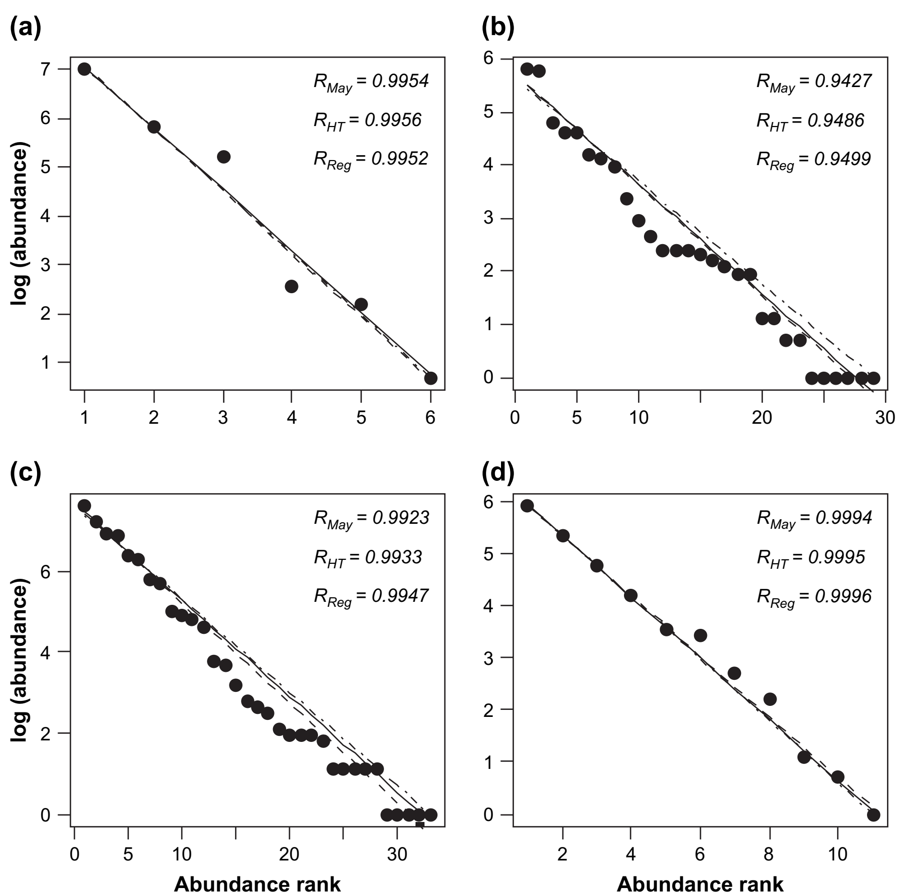

Fig. 1 – Species-dominance curves of four communities: (a) tree species-abundance distribution of a boreal mixedwood forest of Alberta, (b) Carabid beetle abundance distribution in an aspen dominated forest of Alberta (Niemelä et al., 2002), (c) fungi abundance distribution (Magurran, 1988), and (d) Collembola abundance distribution (Magurran, 1988). The dashed line is the fitting of May's method, the dotted-dashed line is that of the regression method, and the solid line is the method developed in this study. The numbers are Pearson's correlation coefficient.

Eq. (3) is 0.18689. Its estimate from Eq. (2) is 0.176755 and 0.18951 from regression method.

The third and fourth data are from Magurran (1988). The third data set is the abundances of filamentous fungi in the phylloplane of the grass *Lolium perenne* (Fig. 1c). There are 33 species with total of 7861 individuals. The least abundant species has abundance = 1, whereas the most abundant species has abundance = 1988. The k estimated from Eq. (3) is 0.21128; its estimate from Eq. (2) is 0.20625, while it is 0.22003 from the regression method.

The fourth data are the abundances of 11 Collembola species (Magurran, 1988) (Fig. 1d). Its total abundance = 862. The least abundant species has one organism and the most abundant species has 370 organisms. The k estimated from Eq. (3) is 0.44642; its estimates from Eq. (2) and the regression method are 0.44906 and 0.44156, respectively.

Fig. 1 shows the observed and fitted dominance curves of the four data. Note that the lines are not regression lines. Instead, they are the fitted abundance calculated by substituting the respective estimated k into Eq. (1). The adequacy of the three methods is evaluated by Pearson's correlation coefficient between the observed and fitted abundances, rather than the coefficient of determination (R^2) resulting from regression. This is because (1) both Eqs (2) and (3) are not involved in regression and (2) our ultimate interest is how well the methods describe abundance not the log-transformed abundance. All the three methods model the data very well. Although the regression method performs slightly better and May's method is slightly worse than the method developed here, their difference in terms of the correlation coefficient is very small. While any of them can be used to parameterize the niche preemption model, Eq. (3) is obviously simpler than the other two. Different from Eq. (2), Eq. (3) does not involve community size N. This means that for a geometric series community if the minimum and maximum abundances as well as the number of species are given, then the niche partition of the community is completely determined.

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