



Review

An improved neutral community model for temporal observations in microbial communities

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ABSTRACT

Niche theory and neutral theory propose two alternative mechanisms for explaining the long-term coexistence of species in ecological communities. However, the true dynamic mechanisms of ecological communities likely fall in between these two theories of niches and neutrality. Thus, models reconciling the niche and neutral theories to interpret these mechanisms are of high significance. Using temporal observations of microbial communities, Ofițeru et al. (2010) demonstrated a version of the neutral community model that quantifies the contributions of neutral forces and environmental factors on the population dynamics of species in the community. They use a novel weighted least squares method to estimate the parameters. However, this method estimates compound parameters and the population size cannot be disentangled from the immigration rate, becoming computationally intractable when there are zero values existing in the temporal observations. In the current study, we suggest a new version of the neutral community model, modified from the work of Ofițeru et al. that does not suffer from these limitations. We also provide a new method for estimating the parameters for our model, which can resolve the estimates of individual parameters. We apply the new model to a real data set and compare our results with those of Ofițeru et al.

1. Introduction

The basic driving forces that shape ecological communities have under debate for a long time. Traditionally, niche theory (MacArthur and Levins, 1967; Chesson, 2000; Chase and Leibold, 2003) suggests that niche partitioning enhances competition with conspecific individuals, and species limit their own populations more than those of other species, providing a stabilization mechanism which assembles ecological communities, but it fails to interpret why there are so many rare species coexisting in tropical forests (Hubbell, 2001). Alternatively, the neutral theory of biodiversity (Bell, 2001; Hubbell, 2001) disregards differences among species and hypothesizes functional equivalence at the individual level. Within the neutral theory, stochastic process is the leading ecological force, and the coexistence of species is the result of a dynamic balance between birth/immigration and extinction. An advantage of the neutral theory is that it yields analytical predictions for ecological patterns, such as species abundance distribution (Hubbell, 2001; Rosindell et al., 2011). These prediction patterns have shown to be successful with real data, especially in tropical forests (Hubbell, 2001; Volkov et al., 2003, 2005). Thus, neutral theory has prevailed over the past sixteen years; however, a growing body of evidence shows

that neutral theory and niche theory can respectively yield similar predictions of biodiversity patterns (Chave et al., 2002; Purves et al., 2005; Noble and Fagan, 2015). It is more likely that both niche and neutral mechanisms play roles in real ecological communities (Stokes and Archer, 2010), and several researchers have proposed the reconciliation of these two theories (Leibold and McPeck, 2006; Gravel et al., 2006; Adler et al., 2007; Kadmon and Allouche, 2007). However, we have found that these synthesized works mostly focus on spatial patterns, and it is very difficult to mathematically analyze such mixed models that rarely apply to real data sets (Tilman, 2004). In addition, neutral theory also can yield explicit predictions about the evolution of communities over time, but an appropriate framework for temporal observations still has not been established, so very little work has been done in this area (Rosindell et al., 2011; Etienne et al., 2007; Gilbert et al., 2006; Vanpeteghem et al., 2008; Keil et al., 2010). However, using observations in a time series, we can study the effects of neutrality caused by environmental change, and these temporal observations could provide more information for inferring dynamic mechanisms of ecological communities (Wells et al., 2009). In addition, if we want to describe the dynamic variations of a whole community, traditional statistical models (e.g., multivariate autoregressive model) are

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too complex because many of the parameters must be estimated (Etienne et al., 2007). Under most circumstances, the samples are not large enough to estimate these parameters. Thus, to benefit from temporal samples while simplifying the model, we can attempt to model only the dynamic variations of single species. Under the conditions of neutral assumptions (Hubbell, 2001), Ofițeru et al. (2010) demonstrated a neutral community model for a single operational taxonomic unit (OTU) within a microbial community based on previous works. The transition matrix of the model is similar to Hubbell's, but has been extended for use with microbial communities into a continuous format, and incorporates environmental effects. With the continuous format, the dynamic variation of single species is viewed as a diffusion process and can be represented by a stochastic differential equation. To estimate the parameters, the authors transformed the stochastic differential equation into a linear regression model and suggested a weighted least squares method. However, because the current technology for detecting microorganisms has detection limits (Curtis et al., 2002), the species in the microbial community cannot be detected; consequently, there are zero values in the observation dataset. Unfortunately, the models from Ofițeru et al. (2010) cannot contend with a dataset of temporal observations with zero values. Although this limitation can be partly overcome by high-quality data, along with further development of molecular technology, the authors neglect one situation. The individuals of the species are all dead at the time of sampling in the local community, so that they cannot be detected; therefore, it is still necessary and significant to be able to model the temporal observations of the microbial community with zero values at this situation. In addition, local community size and immigration rate are mixed in their model. However, the immigration rate is important for analyzing the diversity of ecological communities. As a result of our analysis of this model, we would like to propose a more general neutral community model to improve the utilization of temporal observations within microbial communities. Inspired by previous works (Sloan et al., 2006; Burns et al., 2015), we have also provided a new parametric estimation method. Different with weighted least squares method, the individual parameters can be inferred from our method, and the abovementioned shortcomings have been resolved.

2. Materials and methods

2.1. A broader neutral community model for temporal observations

The main notations and the core concepts of our model were originally introduced by Sloan et al. (2006) and Ofițeru et al. (2010). In this study, we are introducing a necessary derivation to the model. We make the following assumptions: (1) the local community with N_T individuals varies as an assemblage; (2) at a species-independent rate, an individual dies, or leaves the local community, then the position of this individual is replaced either by an immigrant from a source community with the probability m , or by the reproduction of a member in the local community with probability $1 - m$; (3) the relative abundance of the species that the individual belongs to is p in the source community; therefore, the evolution of the whole local community is driven by a series of immigration, birth, and death processes. By choosing a time period in which only one individual death occurs, one species with initial abundance N will have three possible states (increase by one, stay the same, or decrease by one) in the next time period. The corresponding transition probability can be given by the following expressions (Sloan et al., 2006; Ofițeru et al., 2010):

$$\Pr(N + 1/N) = \left(\frac{N_T - N}{N_T}\right) \left[mp + (1 + \alpha)(1 - m) \left(\frac{N}{N_T - 1}\right) \right], \quad (1)$$

$$\Pr(N - 1/N) = \left(\frac{N}{N_T}\right) \left[m(1 - p) + (1 + \alpha)(1 - m) \left(\frac{N_T - N}{N_T - 1}\right) \right], \quad (2)$$

$$\Pr(N/N) = 1 - \Pr(N + 1/N) - \Pr(N - 1/N), \quad (3)$$

where α is a parameter that can confer advantage ($\alpha \neq 0$) or disadvantage ($\alpha = 0$) on the birth rate of a species. When., it is assumed that environmental factors have effects on the birth rates of species. Thereby the parameter α controls the transition from niche-dominated to neutral regime. If the relative abundance of one species in a local community is represented as $x = N/N_T$, and N_T is large enough, then x can be considered as a continuous variable. Let a be the mean time for one replacement in a local community, then scale time t by a to be $\tau = t/a$. Consequently, in a time period $\Delta\tau$, the expected changes in x are $\Delta x = \pm 1/N_T$, 0. Then, the expectation and squared difference for x can be calculated as (Sloan et al., 2006; Ofițeru et al., 2010):

$$E(\Delta X|X = x) = \frac{1}{N_T} [(m - p)x + 2\alpha(1 - m)x(1 - x)], \quad (4)$$

$$E(\Delta X^2|X = x) = \frac{1}{N_T^2} [2(1 - x)x + m(p - x)(1 - 2x)]. \quad (5)$$

Next, the dynamic variations of the species can be considered as a diffusion process. According to mathematical theory, we can refer to Eq. (4) as the drift term and Eq. (5) as the diffusion term to get a non-linear stochastic differential equation:

$$dx = N_T(m(p - x) + 2\alpha(1 - m)x(1 - x))\Delta\tau + \sqrt{2(1 - x)x + m(p - x)(1 - 2x)}dw_\tau, \quad (6)$$

where $\Delta\tau = 1/N_T^2$, w_τ is standard Brownian motion.

Substituting $\tau = t/a$ into Eq. (6), we get

$$dx = N_T(m(p - x) + 2\alpha(1 - m)x(1 - x))\frac{dt}{a} + \frac{1}{\sqrt{a}}\sqrt{2(1 - x)x + m(p - x)(1 - 2x)}dw_t, \quad (7)$$

where α can be a linear function of k observed factors $\{Z_i\}_{i=1}^k$, such as $\alpha = a_0 + \sum_{i=1}^k a_i Z_i$.

Further, under assumption of neutrality ($\alpha = 0$), Eq. (7) becomes

$$dx = N_T m(p - x)\frac{dt}{a} + \frac{1}{\sqrt{a}}\sqrt{2(1 - x)x + m(p - x)(1 - 2x)}dw_t. \quad (8)$$

Eqs. (7) and (8) are our central formulas and the token of our neutral community model.

The model of Ofițeru et al. (2010) consists of the following two formulas:

$$dx = N_T(m(p - x) + 2\alpha(1 - m)x(1 - x))\frac{dt}{a} + \frac{1}{\sqrt{a}}\sqrt{2(1 - x)x}dw_t, \quad (9)$$

$$dx = N_T m(p - x)\frac{dt}{a} + \frac{1}{\sqrt{a}}\sqrt{2(1 - x)x}dw_t. \quad (10)$$

Comparing these with our central formulas [Eqs. (7) and (8)], the difference is that term $m(p - x)(1 - 2x)$ is absent in the Ofițeru et al. model [Eqs. (9) and (10)]. To discuss this easily, we refer to Eqs. (7) and (9) as the non-neutral community model and Eqs. (8) and (10) as the purely neutral community model.

2.2. The method of parameter estimation

Directly implementing Maximum Likelihood Estimator (MLE) for the parameters of our model [Eqs. (7) and (8)] is somewhat difficult. Thus, the likelihood estimation for parameters of our model will be implemented following the steps below:

i. Estimation of N_T and p . Average over all observed communities (samples) to get estimation of N_T . That is $\hat{N}_T = \frac{1}{n} \sum_{k=1}^n N_k$, where n is the number of local communities and N_k is the number of individuals in the k th community. The relative abundance p for one species in the source community can be calculated as $\hat{p} = \frac{1}{nN_T} \sum_{k=1}^n A_k$, where A_k is

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