



Short communication

Local speciation can be incorporated into neutral theory of biodiversity



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ABSTRACT

In this report, I incorporate local speciation into neutral theory of biodiversity to predict species abundance distribution patterns. By fitting the local-speciation model to the abundance data of tree species in Barro Colorado Island of Panama, the results showed that the new model performed better than the original neutral model without local speciation. Moreover, the estimated local speciation rate ($\nu' = 0.0107$) was found to be ten-fold larger than the estimated background speciation rate ($\nu = 0.0011$), indicating that local speciation should not be ignored in neutral theory. Given that species across different local habitats and landscapes may present heterogeneous speciation rates, it is valuable to incorporate local speciation into neutral theory to study spatiotemporal patterns of ecological assemblages.

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1. Introduction

Since Stephen Hubbell published his book (Hubbell, 2001), neutral theory of biodiversity has represented an important advance for modern community ecology. Neutral theory has been proposed to describe spatiotemporal patterns of ecological communities (Alonso and McKane, 2004) and has been successfully applied to describe species abundance distribution (SAD) patterns. In addition to numerical simulation originally employed in Hubbell (2001), analytical calculation formulas have been extensively developed over the past decade (Volkov et al., 2003, 2007; Etienne and Alonso, 2005; Etienne, 2007).

Three biogeographical processes, namely speciation, immigration and extinction, are major factors shaping insular diversity patterns (Whittaker et al., 2008). However, their relative importance is not equivalent. In most cases, immigration and extinction are the dominant mechanisms stemmed from island biogeography theory (MacArthur and Wilson, 1967; Chen, 2015a). By contrast, speciation is often assumed to be small and slow (Heaney, 2000). However, some other works found that local speciation can contribute substantially to island diversity (Losos, 2010). In particular, on large islands, ecologists believed that radiation or phylogenetic diversification could increase island diversity (Heaney, 2000; Losos and Schluter, 2000). This is because the opening of ecological

opportunities (or empty niches) in these islands (Algar and Losos, 2011). Based on these empirical observations, local speciation has been integrated in island biogeography models (Chen and He, 2009; Chen, 2015a).

However, in the context of neutral theory of biodiversity, the role of local speciation is unclear. In addition to drift, background speciation, immigration and extinction (Volkov et al., 2003; Chen, 2015b), Can local speciation contribute to the prediction and interpretation of SAD patterns in empirical data sets? To address this question, in the present study, I explicitly incorporate local speciation into the sampling formulas for neutral theory and test the fitting power of new sampling formulas on empirical SADs by comparing it to the original formula without the involvement of local speciation.

2. Methods and materials

2.1. A neutral model with local speciation

In this section, I deduce the sampling formula for the neutral model with local speciation. The model has an origin from the original neutral model, the corresponding stochastic master equation of which is governed by the following birth-death process:

$$\frac{dP_n}{dt} = A_{n-1}P_{n-1} + C_{n+1}P_{n+1} - (A_n + C_n)P_n \quad (1)$$

where P_n denotes the probability of a species at time t having abundance n . The coefficients A_n and C_n are the birth and death rates

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for the probability when the species has the abundance n . For the proposed local-speciation neutral model in the present study, they are calculated as follows,

$$\begin{cases} A_n = \frac{J-n}{J} \frac{n}{J-1} (1-m-v') + \frac{J-n}{J} m\omega \\ C_n = \frac{n}{J} v' + \frac{(J-n)n}{J(J-1)} (1-m-v') + \frac{n}{J} m(1-\omega) \end{cases} \quad (2)$$

Without further notation hereafter, J denotes the local community size. m is the regional immigration rate of species from the metacommunity. ω is the relative abundance of species in the meta-community. The new parameter presented in Eq. (2) is the local speciation rate v' , which reflects the influence of local speciation on the stochastic birth-death process of the neutral model. When there is no local speciation (i.e., $v' = 0$), the transition probabilities in Eq. (2) become identical to those presented in previous studies (Vallade and Houchmandzadeh, 2003; Volkov et al., 2003).

Here I further set the following quantities,

$$\begin{cases} r = \frac{J-1}{1-m-v'} m \\ s = \frac{J-1}{1-m-v'} v' \\ \lambda = \frac{J-1}{1-m-v'} m\omega \end{cases} \quad (3a)$$

where r here represents the strength of regional dispersal, while s represents the influence of local speciation. Their relation is given by $s/r = v'/m$. This ratio thus depends on the relative strength of local speciation and regional immigration. Based on these definitions, it can be further seen that,

$$\begin{cases} \lambda = \omega r \\ s = r \frac{v'}{m} \end{cases} \quad (3b)$$

Then, by using the quantities in Eqs. ((2), (3a) and (3b)), Eq. (1) at equilibrium can be solved as,

$$P_n(\omega) = \binom{J}{n} \frac{(r\omega)_n (s+r(1-\omega))_{J-n}}{(s+r)_J} \quad (4)$$

This is the typical form of local sampling formula established previously (Vallade and Houchmandzadeh, 2003; Alonso and McKane, 2004; Etienne and Alonso, 2005). Eq. (4) uses the notation for Stirling number as $(a)_n = a(a+1) \dots (a+n-1)$. So, the expected species with abundance n in the local sample is given by,

$$E[S_n|\theta, r, s, J] = \int_0^1 \binom{J}{n} \frac{(r\omega)_n (s+r(1-\omega))_{J-n}}{(s+r)_J} \times \theta \frac{(1-\omega)^{\theta-1}}{\omega} d\omega \quad (5)$$

where θ denotes the fundamental biodiversity number (Hubbell, 2001; Alonso and McKane, 2004; Volkov et al., 2003). The background speciation rate v mentioned above is integrated in this parameter as $\theta = 2J_M v$ (Hubbell, 2001; Alonso and McKane, 2004). Here J_M is the metacommunity size.

Alternatively, one can use an approximate sampling equation presented in Volkov et al. (2003, 2007), in which the probability of a species with abundance n is given by,

$$\begin{aligned} P(n) &= \binom{J}{n} \frac{\Gamma(n+\lambda)}{\Gamma(1+\lambda)} \frac{\Gamma(J+r-\lambda+(r/m)v'-n)}{\Gamma((r/m)v'+r-\lambda)} \frac{\Gamma((r/m)v'+r)}{\Gamma((r/m)v'+J+r)} \\ &= \binom{J}{n} \frac{\Gamma(n+r\omega)}{\Gamma(1+r\omega)} \frac{\Gamma(J+r-r\omega+s-n)}{\Gamma(s+r-r\omega)} \frac{\Gamma(s+r)}{\Gamma(s+J+r)} \end{aligned} \quad (6)$$

where $\Gamma(\bullet)$ denotes the Gamma function as $\Gamma(t) = \int_0^\infty x^{t-1} e^{-x} dx$. The second equality in (6) used the quantities presented in Eq. (3b).

The expected value of species with abundance n in the community is then calculated approximately as,

$$\begin{aligned} E[S_n|\theta, r, s, J] &= \theta \int_0^1 \binom{J}{n} \frac{\Gamma(n+r\omega)}{\Gamma(1+r\omega)} \frac{\Gamma(J+r-r\omega+s-n)}{\Gamma(s+r-r\omega)} \frac{\Gamma(s+r)}{\Gamma(s+J+r)} e^{-\omega\theta} d\omega \end{aligned} \quad (7)$$

When $s=0$ (thus $v'=0$, no local speciation), the above Eq. (7) is identical to the formula presented in Volkov et al. (2003). The integral in this equation can be done numerically so to compute the expected number of species with abundance n .

Maximum likelihood method for estimating parameters

To fit the model to empirical data sets, I employ the maximum likelihood model used in the previous studies (Alonso and McKane, 2004; Etienne and Alonso, 2005) as,

$$\begin{aligned} L(\text{Data}|\theta, r, s, J) &= p(1)^{S_1} \dots p(a)^{S_a} \\ p(n) &= \frac{E[S_n|\theta, r, s, J]}{\sum_{i=1}^J E[S_i|\theta, r, s, J]} \end{aligned} \quad (8)$$

$$-\text{Log}(L(\text{Data}|\theta, r, s, J)) = -\sum_{i=1}^a S_i \text{Log}(p(i))$$

here $p(n)$ is the normalized probability of a species with n individuals. $E[S_n|\theta, r, s, J]$ is the expected number of species with n individuals calculated from Eq. (7). a is the maximum abundance found in the local community. S_k ($k = 1, 2, \dots, a$) is the observed species number with abundance k in the empirical data set.

2.2. An empirical test

Now it is ready to test the local speciation model and compare it to the original neutral model (i.e., the model without local speciation by setting $s=0$). Tree abundance data for Barro Colorado Island (BCI) permanent forest plots in Panama (<http://ctfs.arnarb.harvard.edu/webatlas/datasets/bci/>) were used as an empirical test as previous studies (Alonso and McKane, 2004; Etienne, 2007). Because it is time-consuming to compute Stirling number in Eq. (5), I estimated the parameters (θ , r , and s) using the maximum likelihood model derived from Eq. (7). The integral was calculated numerically using the standard trapezoidal rule.

For comparing alternative models and choosing a better model to characterize SAD pattern of BCI tree species, I utilize the modified Akaike information criterion (AICc) (Akaike, 1974; Haining, 2003; Chen, 2013) accounted for small samples as follows,

$$\text{AICc} = -2(m-1)\text{Log}(L) + 2k \frac{m-1}{(m-1)-k-1} \quad (9)$$

where $\text{Log}(L)$ is the log-transformed likelihood value as in Eq. (8), m is the number of data points used for maximizing the likelihood as above and k is the number of parameters presented in the model.

3. Results

The maximum likelihood estimation of parameters could be best achieved at $\theta = 47.6179$, $r = 1879.94$, and $s = 252.401$ (Table 1). This local speciation model had AICc = 2612.126. In contrast, for the model without local speciation (by mandatorily setting $s=0$ in Eq. (7)), the fitted parameters became $\theta = 46.625$ and $r = 2288.86$, respectively (Table 1). These estimated values were very similar to

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