



## Species ages in neutral biodiversity models



Ryan A. Chisholm<sup>a,\*</sup>, James P. O'Dwyer<sup>b,c</sup>

<sup>a</sup> Department of Biological Sciences, National University of Singapore, 117543, Singapore

<sup>b</sup> Santa Fe Institute, Santa Fe, NM 87501, USA

<sup>c</sup> Department of Plant Biology, University of Illinois, Urbana, IL 61801, USA

### ARTICLE INFO

#### Article history:

Received 6 May 2013

Available online 12 February 2014

#### Keywords:

Biodiversity  
Biogeography  
Species ages  
Neutral theory  
Population genetics  
Neutral molecular evolution

### ABSTRACT

Biogeography seeks to understand the mechanisms that drive biodiversity across long temporal and large spatial scales. Theoretical models of biogeography can be tested by comparing their predictions of quantities such as species ages against empirical estimates. It has previously been claimed that the neutral theory of biodiversity and biogeography predicts species ages that are unrealistically long. Any improved theory of biodiversity must rectify this problem, but first it is necessary to quantify the problem precisely. Here we provide analytical expressions for species ages in neutral biodiversity communities. We analyse a spatially implicit metacommunity model and solve for both the zero-sum and non-zero-sum cases. We explain why our new expressions are, in the context of biodiversity, usually more appropriate than those previously imported from neutral molecular evolution. Because of the time symmetry of the spatially implicit neutral model, our expressions also lead directly to formulas for species persistence times and species lifetimes. We use our new expressions to estimate species ages of forest trees under a neutral model and find that they are about an order of magnitude shorter than those predicted previously but still unrealistically long. In light of our results, we discuss different models of biogeography that may solve the problem of species ages.

© 2014 Elsevier Inc. All rights reserved.

### 1. Introduction

The problem of species ages is central to biogeography. A species' age is the amount of time elapsed since the species arose through speciation. Species ages can be inferred from the fossil record or phylogenies. What determines the distribution of species ages observed in nature? A null hypothesis is that the distribution of species ages is determined by the process of random drift. On this view, following a speciation event a species' abundance simply drifts randomly with demographic stochasticity and eventually reaches zero, at which time the species goes extinct. This hypothesis of random drift is a central tenet of the neutral theory of biodiversity and biogeography, a theory that has successfully predicted static patterns of biodiversity, especially in high-diversity communities (Condit et al., 2012; Hubbell, 2001; Leigh, 2007; O'Dwyer and Green, 2010; Volkov et al., 2003). Neutral theory, however, apparently fails to reproduce empirically observed species ages. Indeed, previous neutral predictions of species ages have exceeded even the age of the Earth (Nee, 2005).

It is worth taking a moment to discuss the difference between 'species age' and 'species lifetime' (Rosindell et al., 2011), because this can be potentially confusing. The age of a species at a given time is simply the amount of time that has elapsed since its moment of origin (the speciation event). Species lifetime, on the other hand, refers to the amount of time between the speciation event and the extinction event. One way to think of it is that species lifetime is a special case of species age: species lifetime is the age of a species at the moment it goes extinct. Our main focus here is on species ages rather than species lifetimes, although we do produce a species lifetime formula as a special case and we return to the distinction between species ages and species lifetimes in the Discussion.

Estimates of neutral species ages in a biodiversity context have previously been based on simulations (Hubbell, 2001, Chapter 8) or on analytical approximations drawn from the neutral theory of molecular evolution, which describe the expected age of an allele (i.e., the time since the allele arose through mutation) as a function of the allele's current relative abundance (Kimura, 1983; Kimura and Ohta, 1973; Nee, 2005). However, while similar mechanisms apply in both the neutral theory of molecular evolution and the neutral theory of biodiversity, the molecular evolution results have previously been applied to biodiversity problems in an inappropriate parameter regime. This is firstly because the results are based

\* Corresponding author.

E-mail address: [ryan.chis@gmail.com](mailto:ryan.chis@gmail.com) (R.A. Chisholm).

on the assumption that mutation is so infrequent that a new allele either goes extinct or to fixation before another mutation can occur, and secondly because the particular results adapted and applied to neutral biodiversity theory (Nee, 2005) condition on alleles not having reached fixation; in effect, the underlying model stops tracking an allele when it reaches fixation. In the language of biodiversity, these assumptions would mean that speciation is so infrequent that a new species either goes extinct or comes to dominate the entire community before another speciation event occurs. These formulas may be applicable to the special case of ecological communities where complete dominance by one species is typical and where a second species can meaningfully be identified as a newer, mutant species, by analogy with the mutant allele. In most ecological communities, however, complete dominance by any one species is unusual. In tropical forests, for example, hundreds of tree species may coexist within a few hectares (Leigh et al., 2004) and even in temperate forests at least five or ten species may do so. In such contexts, we need species age formulas that assume a non-negligible probability of speciation in evolutionary time, and we can dispense with the distinction between resident and mutant types.

Our goal here is to derive exact neutral species age formulas that are applicable to biodiversity problems, in line with the issues raised above. We do this first for a non-zero-sum model and then for a zero-sum model. Our strategy is to start with the standard master equations of neutral biodiversity models and then to apply novel mathematical approaches to get the species age formulas. We then show how our species age formulas relate to previous formulas taken from the neutral theory of molecular evolution.

**2. Non-zero-sum model**

*2.1. Master equation*

Consider a community of individuals in which the probability of any given individual dying in a short period of time  $\Delta t$  is equal to  $\Delta t$  and the probability of an individual reproducing in a period  $\Delta t$  is also  $\Delta t$  (so time is measured in units of generations, where a generation is the average age difference between an offspring and its parent). When an individual reproduces, its offspring may mutate to a new species, with probability  $\nu$ . Because birth and death events occur independently in this model, the community size is not fixed (i.e., the system is not zero-sum) but fluctuates around some mean value, which we call  $J$ . The system is described by the following birth–death master equation:

$$\frac{dP(n, t)}{dt} = (1 - \nu) ((n - 1)P(n - 1, t) - nP(n, t)) + (n + 1)P(n + 1, t) - nP(n, t) \tag{1}$$

where  $P(n, t)$  is the probability that a species has abundance  $n$  at time  $t$ , and  $t$  is measured in generations. We will also impose the initial condition  $P(n, 0) = \delta_{n,1}$ , where  $\delta_{i,j}$  is the Kronecker delta, meaning that a newly created species has only one individual (i.e., this is a model of point speciation).

*2.2. Abundances*

We first derive a general expression from (1) that gives the transition probability  $X_{jk}(t)$  of having abundance  $j$  at time  $t$ , given that the abundance at time zero was  $k$  (Appendices A and B):

$$X_{jk}(t) = \left( \frac{1}{\omega(t)\Omega(t)} + 1 \right)^{-j} \times (\Omega(t) (1 + \omega(t)\Omega(t)))^{-k} \binom{j+k-1}{j} \times {}_2F_1(1-k, -k, 1-k-j; (1-\Omega(t))(1+\omega(t)\Omega(t))) \tag{2a}$$

for  $j > 0$  (where  ${}_pF_q$  is the generalised hypergeometric function), and

$$X_{0k}(t) = \left( 1 - \frac{\omega(t)}{1 + \Omega(t)\omega(t)} \right)^k \tag{2b}$$

where

$$\omega(t) = \exp(-\nu t) \quad \Omega(t) = \left( \frac{1}{\omega(t)} - 1 \right) \frac{1 - \nu}{\nu}.$$

We expect these new results (2) to be very useful in neutral ecology because they express the probability of going from one arbitrary abundance  $k$  to another arbitrary abundance  $j$  in  $t$  generations. In this paper though, our specific focus is on species ages in a point speciation model and henceforth we take the special case  $k = 1$  so that  $t$  represents the amount of time that has elapsed since the point speciation event that gave rise to the focal species.

*2.3. Species ages*

To derive an expression for the mean species age  $T_n^*$ , given abundance  $n$ , in the model described by (1) we write (Appendix C)

$$T_n^* = E(T|N = n) = \frac{\int_{t=0}^{\infty} tP(n, t)dt}{\int_{t=0}^{\infty} P(n, t)dt} \tag{3}$$

To simplify this, we note that  $P(n, t) = X_{n1}(t)$ , because it is the probability of having  $n$  individuals at time  $t$  given that there was 1 individual at time zero (point speciation). The integral on the denominator of (3) is equal to the species abundance distribution  $\phi(n)$  divided by a constant  $J\nu$ . We can evaluate this species abundance distribution integral by first noting that  $X_{jk}(t)$  takes a special form when  $k = 1$  (Appendix D), leading to

$$\phi(n) = \frac{1}{n} \frac{J\nu}{1 - \nu} (1 - \nu)^n. \tag{4}$$

This is the log-series abundance distribution (Fisher et al., 1943), which has previously been derived for neutral biodiversity models using a variety of mathematical approaches (e.g., Alonso and McKane, 2004; Volkov et al., 2003).

The numerator on the right-hand side of expression (3) is a more difficult integral but can nonetheless be evaluated (Appendix D), leading ultimately to the species age formula:

$$T_n^* = \frac{1}{\nu} \left\{ \left( \frac{1}{1 - \nu} \right)^n B(1 - \nu; 1 + n, 0) + H_n + \log(\nu) \right\} \tag{5}$$

where  $B(z; a, b)$  is the incomplete beta function and  $H_n$  is a harmonic number (Abramowitz and Stegun, 1972). Eq. (5) gives the exact mean species ages in the neutral model described by Eq. (1) and constitutes the first of two main results of this paper. For  $n\nu \gg 1$ , the term with the beta function goes to zero and  $H_n$  can be approximated as  $\gamma + \log(n)$ , where  $\gamma$  is the Euler–Mascheroni constant, leading to the following asymptotic result:

$$T_n^* \sim \frac{1}{\nu} \{ \gamma + \log(n\nu) \}. \tag{6}$$

In the opposite limit, where  $n\nu \ll 1$ , we have another asymptotic result:

$$T_n^* \sim n \{ 1 - H_n - \log(\nu) \}. \tag{7}$$

For a given value of  $\nu$ , these asymptotic solutions provide good approximations for high and low  $n$ , respectively, and are easier to compute numerically (Fig. 1).

Download English Version:

<https://daneshyari.com/en/article/4502345>

Download Persian Version:

<https://daneshyari.com/article/4502345>

[Daneshyari.com](https://daneshyari.com)