

# Speciation Rates Decline through Time in Individual-Based Models of Speciation and Extinction

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**ABSTRACT:** A well-documented pattern in the fossil record is a long-term decline in the origination rate of new taxa after diversity rebounds from a mass extinction. The mechanisms for this pattern remain elusive. In this article, we investigate the macroevolutionary predictions of an individual-based birth-death model (BD<sub>i</sub> model) where speciation and extinction rates emerge from population dynamics. We start with the simplest neutral model in which every individual has the same per capita rates of birth, death, and speciation. Although the prediction of the simplest neutral model agrees qualitatively with the fossil pattern, the predicted decline in per-species speciation rates is too fast to explain the long-term trend in fossil data. We thus consider models with variation among species in per capita rates of speciation and a suite of alternative assumptions about the heritability of speciation rate. The results show that interspecific variation in per capita speciation rate can induce differences among species in their ability to resist extinction because a low speciation rate confers a small but important demographic advantage. As a consequence, the model predicts an appropriately slow temporal decline in speciation rates, which provides a mechanistic explanation for the fossil pattern.

**Keywords:** speciation rate, origination rate, macroevolution, neutral theory, birth-death models.

## Introduction

One remarkable pattern revealed by the fossil record is the long-term decline in the origination rate of new taxa following the rebound of diversity after a mass extinction (Sepkoski 1998; Alroy 2008). This declining pattern has been shown to be robust to the choice of rate metrics and taxonomic groups (Gilinsky and Bambach 1987; Benton 1995; Foote 2003; Alroy 2008). The temporal decline in the per taxon origination rate is also supported by evidence

from molecular phylogenetic studies, which have often detected a pattern of “explosive-early diversification” (McPeck 2008; Rabosky and Lovette 2008; Morlon et al. 2011). One explanation for the decline relies on niche mechanisms which treat speciation as an ecologically adaptive process. Innovation-driven adaptive radiations may cause an increase in speciation rate while niches are being filled by the new innovation (Etienne and Haegeman 2012). However, opportunities for speciation subsequently become reduced once niches are filled (Alroy 2008; Ricklefs 2010). This niche perspective has been challenged by at least two facts. First, taxon origination can slow even if biodiversity holds relatively constant (Sepkoski 1998; Alroy et al. 2008). Second, niche-based mechanisms are unlikely to apply to nonecological (or nonadaptive) speciation, which is presumed to be common (Heard and Hauser 1995; Hubbell 2001; Leibold and McPeck 2006; Rundell and Price 2009).

Alternatively, the taxon selection hypothesis suggests that the decline in speciation rates results from the replacement of early dominant high-speciation-rate taxa by those with lower rates (Sepkoski 1998; Alroy 2008). For instance, by simulating the evolution of clades with different macroevolutionary rates, Gilinsky (1994) found that clades with high rates of speciation and extinction were prone to become extinct due to their volatile dynamics, hence leaving groups with low rates to accumulate over time. This hypothesis strongly relies on the assumption of a correlation between the rates of speciation and extinction (Gilinsky 1994), which is supported by empirical data (Stanley 1975) but lacks a clear mechanism. Without such a correlation, species selection should favor the accumulation of high-speciation-rate species and consequently cause the total speciation rate of the community to increase (Heard 1996; Mooers et al. 2007). Therefore, a more mechanistic model is required to explain the correlation between

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rates of speciation and extinction and the temporal decline in speciation rates.

Stochastic models of branching processes have long been used in understanding macroevolutionary patterns (Raup et al. 1973; Nee et al. 1994; Nee 2006). These models are usually formulated at the species level by assigning probabilities of speciation and extinction. Because they are structurally similar to birth-death models of individuals, they are also called birth-death models ( $BD_S$  models, where subscript  $S$  denotes their species-based nature; Nee 2006). Though extremely simple,  $BD_S$  models have proven to be efficient tools for informing macroevolutionary thinking about paleontological and phylogenetic data (reviewed in Nee 2006). One limitation of these models is that they do not explicitly incorporate population dynamics. Both speciation and extinction rates are strongly affected by population size. For example, species with large abundance and/or geographic range are more resistant to extinction than rare species (McKinney 1997; Purvis et al. 2000).

In this article, we investigate the temporal trends in speciation rate predicted by an individual-based birth-death model ( $BD_I$  model), which explicitly incorporates the population dynamics of speciation and extinction. This  $BD_I$  model stems from Hubbell's (2001) neutral theory of biodiversity (NTB), which explains community diversity patterns from speciation and ecological drift (Hubbell 2001; Chave 2004). We will first examine the post-mass-extinction macroevolutionary patterns predicted by Hubbell's original model and then extend this model by allowing interspecific variation in the speciation rate. Variation in speciation rates among lineages has been broadly demonstrated in paleontology and molecular phylogenetics (Sepkoski 1998; Coyne and Orr 2004; Morlon et al. 2011; Stadler 2011). As we will show, interspecific variation in speciation rates in a demographic model can induce variation among species in their ability to resist extinction, select for species with low speciation rates, and ultimately result in a declining trend of the origination rate of new species.

### An Individual-Based Macroevolutionary Model

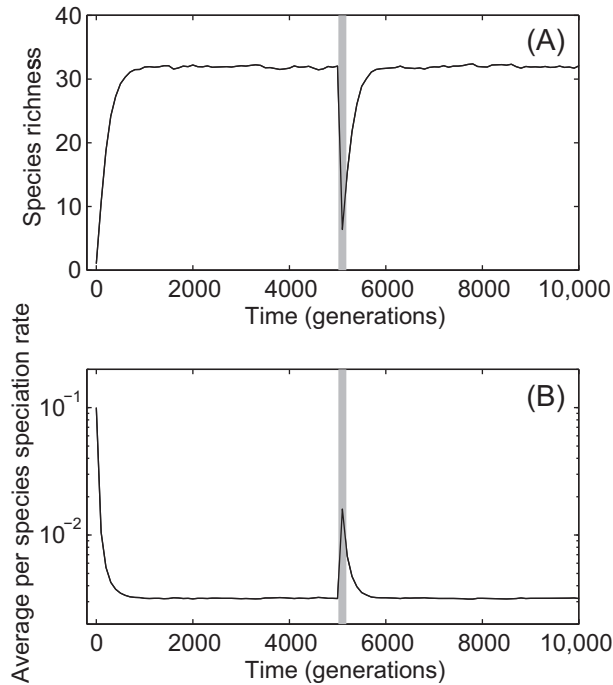
#### *Macroevolutionary Patterns under Neutral Theory*

In Hubbell's (2001) NTB model, the community consists of a fixed number of ecologically equivalent individuals that compete for space in a zero-sum game. In each time step, every individual of every species has the same probability of death and giving birth. Each dead individual is instantly replaced by a random draw from the births. New species are produced randomly. The per-species rate of speciation is proportional to population size because speciation rates are defined per capita (i.e., individuals spon-

taneously mutate into a new species when they are born, or species fission at rates proportional to population size; Hubbell 2001). In contrast, extinction rates are emergent properties of population dynamics: an extinction occurs when the last individual of a species dies before reproducing. Thus, a species' extinction probability depends on its current abundance and per capita birth and death rates (Hubbell 2001, 2005). As a consequence, any ecological and evolutionary processes that affect population dynamics also affect speciation and extinction rates.

We simulated the macroevolutionary dynamics of a neutral community after a mass extinction event. We first ran the NTB model to equilibrium and then randomly killed 80% of the species. After refilling the space by random births, the remaining species had larger per-species speciation rates than before the mass extinction, simply because they had larger average population sizes than before the extinction and because speciation rates are constant per capita in the model (fig. 1). Species diversity then climbed back to the equilibrium of the NTB model, thereby reducing both the average population size and the average per-species rate of speciation (fig. 1). Additional numerical work indicates that the time scale of diversity recovery increases with community size (see app. A; apps. A–E available online, community size = the total number of individuals in the simulation). Four results are easy to show analytically. (1) The average rate of total origination of new species remains constant through time. (2) Changes in average per-species speciation rate are driven solely by changes in the average population size. (3) After the mass extinction, increases in the per-species speciation rate occur as soon as the total number of individuals recovers to pre-mass-extinction levels (i.e., instantaneously in geologic time). (4) The average per-species speciation rate then declines simultaneously as diversity recovers, because it is inversely proportional to the number of species in the community.

In summary, the simple NTB model can generate a pattern qualitatively like that in the fossil data, without any niches or adaptive radiation whatsoever. Neutral population dynamics and random speciation at a constant per capita rate may explain some of the reported spikes and subsequent declines in per-species speciation rates following mass extinctions. However, the model's prediction that the total rate of appearance of new species remains constant is not consistent with the increase and subsequent decline of this quantity after mass extinction implied by the fossil data (Benton 1995; Levinton 2001; Kirchner 2002). Moreover, the fossil record indicates that diversity recovery after a mass extinction usually takes less than 10 million years (Erwin 1998; Kirchner and Weil 2000; Chen and Benton 2012). Thus, the simple NTB model predicts that declines in per-species speciation rates last for no



**Figure 1:** Macroevolutionary dynamics of a neutral community under the random fission speciation mode (Hubbell 2001): species richness (A) and average per species speciation rate (B). Results represent the average of 500 simulations. Parameters: community size  $J = 10,000$ , and per capita speciation rate  $\nu = 10^{-5}$ ; therefore, at each generation, the community will produce on average 0.1 new species. The simulation is performed as follows: starting from an initial species (with abundance of 10,000), the community accumulates diversity gradually to an equilibrium level after 1,000 generations. Then, at the time of the five-thousandth generation (gray vertical line), a mass extinction event is simulated by randomly picking 80% of the species and killing them. Following this, the community size is assumed to increase to  $J$  instantaneously (in one generation) by the population growth of the surviving species. The model is then run for a further 5,000 generations. Notice that after the mass extinction, species diversity undergoes a recovery lasting nearly 1,000 generations before it reaches the pre-mass-extinction level. Note also that the Y-axis in B is logarithmic.

more than 10 million years. This is much shorter than the multi-hundred-million-year decline estimated for the Phanerozoic (Sepkoski 1998; Alroy 2008). For this reason, we now extend Hubbell’s neutral model by incorporating a well-documented pattern of interspecific variation in speciation rate.

*An Extended Individual-Based Birth-Death Model*

The extended  $BD_1$  model retains the assumption of ecological neutrality (that all individuals have the same per capita rates of birth and death) but allows interspecific variation in the per capita speciation rate. Thus, factors

regulating the processes of speciation are assumed to have no influence on ecological fitness; such factors may include sexual selection, hybridization, and vicariance events (Leibold and McPeck 2006; Rundell and Price 2009). The variation in speciation rates results from heritability and lability in speciation rates between parental and daughter lineages, both of which have been demonstrated empirically (Heard 1996; Savolainen et al. 2002; Davies et al. 2004). When speciation is associated with traits that are heritable at the individual level, such as traits affecting sexual selection or animal pollination, speciation rate will also be heritable from ancestral to descendant lineages (Heard 1996; Savolainen et al. 2002). On the other hand, speciation can be nonheritable, for example, when caused by vicariance (Heard 1996; Jablonski 2008).

With this  $BD_1$  model, we study the post-mass-extinction macroevolutionary dynamics of a community with an initial homogeneous per capita speciation rate  $\nu_0$ . When a new species is produced, its per capita speciation rate ( $\nu_{new}$ ) is randomly drawn from a transition probability density. This density depends on the per capita speciation rate of the parent species ( $\nu_{parent}$ ) if the speciation rate is heritable and is independent of  $\nu_{parent}$  if heritability is zero. Hubbell’s (2001) model is a special case of this model with perfect heritability (Hubbell 2001). In this article, we focus on two cases that involve nonperfect heritability in speciation rate: the nonheritable random model ( $M_r$ ) and the partially heritable model ( $M_l$ ). In both cases, we restrict per capita speciation rates within an interval  $[\nu_{min}, \nu_{max}]$ , where  $0 < \nu_{min} < \nu_{max} \ll 1$  and the initial rate  $\nu_0$  is located at the middle of the interval. Under the nonheritable model  $M_r$ ,  $\nu_{new}$  is randomly drawn from a uniform probability density over  $[\nu_{min}, \nu_{max}]$ . Under the partially heritable model  $M_l$ ,  $\nu_{new}$  is uniformly distributed around  $\nu_{parent}$ , that is,  $\nu_{new} \sim U[\nu_{parent} - L/2, \nu_{parent} + L/2]$ , where  $1/L$  is a measure of heritability. To ensure that  $\nu_{new}$  stays within  $[\nu_{min}, \nu_{max}]$ , the uniform distribution is truncated once reaching the outside of the interval. In order to derive the time-dependent solutions of the  $BD_1$  models, we consider the distribution of the per capita speciation rate in a discrete form:  $\{\nu_1, \nu_2, \dots, \nu_n$ , where  $\nu_1 = \nu_{min}$ ,  $\nu_n = \nu_{max}$ , and  $\nu_j - \nu_{j-1} = \text{constant}\}$ . The mathematical expressions for the respective transition probabilities are given in appendix B.

*Analytic Solutions*

For a community with  $J$  individuals and an initial per capita speciation rate  $\nu_0$ , we now derive temporal solutions for the community-averaged per capita speciation rate. We consider three different modes of speciation that differ in the initial population size immediately after speciation: point mutation speciation, fixed fission speciation, and

random fission speciation. The total origination rate of new species is proportional to the average per capita speciation rate because it is the product of this average and the fixed community size  $J$ .

Point mutation is the most commonly used mode of speciation in neutral models. Under point mutation, a new species emerges with an initial abundance of one (Hubbell 2001; Volkov et al. 2003; Chave 2004; Chisholm and Pacala 2010; O'Dwyer and Green 2010), and the time-dependent solution for the relative frequency distribution of per capita speciation rate is (see app. C for derivation)

$$\vec{P}(\tau) = \vec{P}(0) \cdot e^{(\mathbf{VQ}-\mathbf{V})\tau} = \vec{P}(0) \cdot e^{\mathbf{R}\tau}. \quad (1)$$

Here  $\vec{P}(\tau) = (P(v_1, \tau), P(v_2, \tau), \dots, P(v_n, \tau))$ , where  $P(v_i, \tau)$  is the relative frequency of individuals with per capita speciation rate  $v_i$  at time  $\tau$  (unit: generation), and  $\vec{P}(0)$  is the initial value of this vector ( $\vec{P}(0) = (0, \dots, 0, 1, 0, \dots, 0)$ ). The matrix  $\mathbf{R}$  is defined as:  $\mathbf{R} = \mathbf{VQ} - \mathbf{V}$ , where  $\mathbf{V}$  is the diagonal matrix  $\mathbf{V} = \text{diag}(v_1, v_2, \dots, v_n)$  and  $\mathbf{Q} = (q_{ji})$  is the transition matrix in which  $q_{ji}$  is the probability that the newly produced species has per capita speciation rate  $v_i$  given that the rate of its parental species is  $v_j$  (see app. B). Based on equation (1), we can obtain the temporal solution for the average per capita speciation rate:

$$\bar{v}(\tau) = \vec{P}(\tau) \vec{v} = \vec{P}(0) \cdot e^{\mathbf{R}\tau} \cdot \vec{v} \quad (2)$$

where  $\bar{v}(\tau)$  is the average per capita speciation rate in the community at time  $\tau$  and  $\vec{v} = (v_1, v_2, \dots, v_n)$ .

From equations (1) and (2), we learn that the temporal dynamics of the speciation rates are mainly determined by the transition matrix ( $\mathbf{Q}$ ) and the magnitude of speciation rate ( $\mathbf{V}$ ) and are approximately independent of community size. The distribution of per capita speciation rates will converge to an equilibrium that can be expressed by the corresponding eigenvector of the largest eigenvalue of  $\mathbf{R}$  (which is 0), and the tempo of this convergence is determined by a damping ratio defined by the largest two eigenvalues of  $\mathbf{R}$  (see app. C; Coulson and Godfray 2007; Chisholm 2011). Under the nonheritable model ( $M_r$ ), the damping ratio is within the interval  $(e^{v_1}, e^{v_2})$  (see app. C), which implies that the evolutionary tempo should be slow under low speciation rates.

In contrast to point mutation speciation, fission speciation generates new species with average initial abundance larger than one. Hubbell (2001) proposed a random fission mode of speciation, where the parental species is randomly divided into two populations and the smaller one is regarded as the daughter species (see also Etienne and Haegeman 2011). Other neutral models consider a peripheral-isolate model of speciation where new species have a fixed initial abundance (larger than one; Hubbell

2003; Allen and Savage 2007). The peripheral-isolate model is referred to as fixed fission speciation in this article. Under the fixed fission mode, when the initial abundance of the newly produced species ( $n_0$ ) is small relative to the community size ( $J$ ), the temporal dynamics of the average per capita speciation rate can be approximated by (see app. D):

$$\bar{v}_f(\tau) \approx \vec{P}_f(0) \cdot e^{(v_0\mathbf{Q}-v_0)\tau} \cdot \vec{v} \quad (3)$$

Here, subscript  $f$  indicates the fission modes of speciation. A comparison of equations (2) and (3) shows that the temporal evolution of the average per capita speciation rate is  $n_0$  times faster in the fixed fission mode than in the point mutation mode. It is difficult to obtain corresponding analytic solutions under random fission speciation. However, because the average initial abundance of new species under the random fission speciation is larger than  $v_{\max}^{-0.5}/4$ , by substituting  $n_0 = v_{\max}^{-0.5}/4$  into equation (3), we can obtain an estimate of the lower boundary of the evolutionary tempo (see app. D).

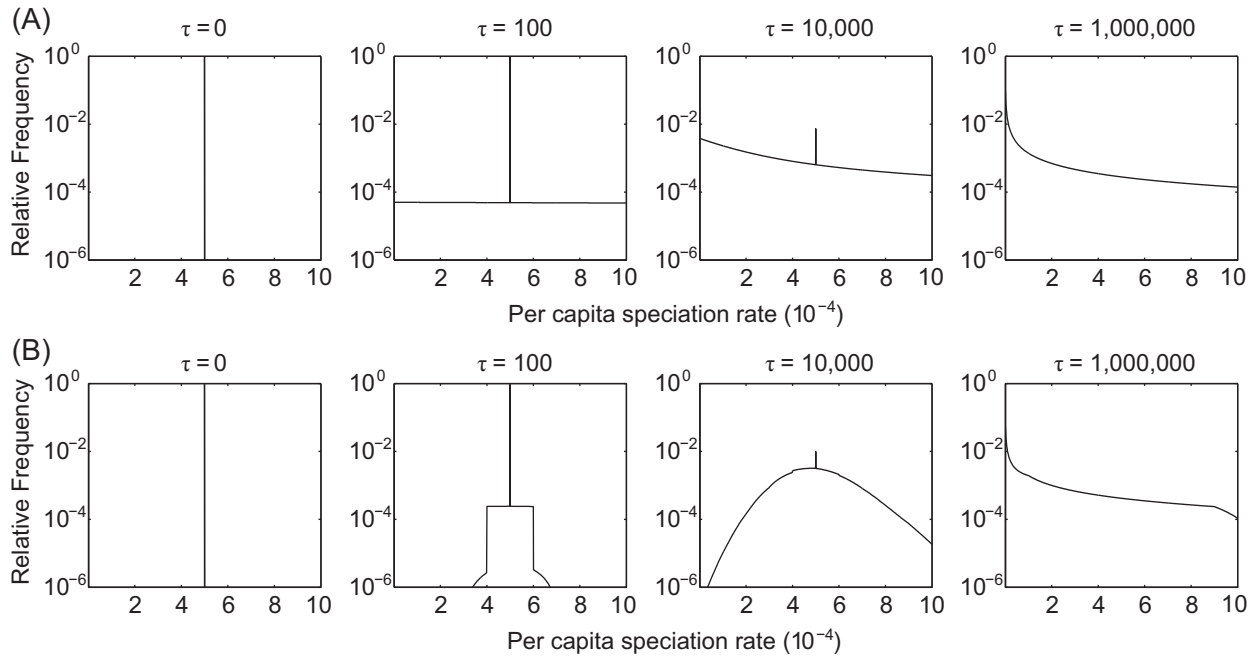
### Simulation Studies

We also performed computer simulations to examine the temporal dynamics of speciation rates. In all simulations, we started with a community consisting of one species with a per capita speciation rate equal to the median of assumed range of values, and simulated the community evolution for 1,000,000 generations, which represents  $\sim 100$  million years if one generation equals about 100 years (Ricklefs 2003). We simulated both random ( $M_r$ ) and partially heritable ( $M_i$ ) models under each of the three speciation modes. In all cases, the simulations were repeated 500 times, and the averaged trajectories of average per capita and per species speciation rates were calculated and compared with analytic solutions. In addition, we investigated the relationship between a species' life span and its per capita speciation rate, by recording the time of origin and extinction of all species in the simulations.

### Results

In both models  $M_r$  and  $M_i$ , high speciation rates are selected against so that relative frequency decreases monotonically with increasing speciation rate (fig. 2). This asymmetry in the frequency distribution evolves gradually but more quickly under the nonheritable model  $M_r$  (fig. 2A) than under the partially heritable model  $M_i$  (fig. 2B).

The macroevolutionary selection against high speciation rates is most easily seen in the long-term declines in the average per capita and average per species speciation rates (fig. 3). The long-term decline in per species speciation



**Figure 2:** Temporal changes in the relative frequency distribution of per capita speciation rate under point mutation speciation under the models  $M_r$  (A) and  $M_t$  (B), based on the analytic equation (1). In both models, the community starts from one species with per capita speciation rate  $v_0 = (v_{\min} + v_{\max})/2$ , where  $v_{\min} = 10^{-6}$  and  $v_{\max} = 10^{-3}$ , and  $L = 2 \times 10^{-4}$  in  $M_r$ . Note that the frequency distribution reaches equilibrium at  $\tau = 1,000,000$  (unit: generation).

rate is caused by the decline of the average per capita rate, not by an increase in species richness (figs. 3 and C3; figs. C1–C4 available online). The decline is amplified by small heritability and a large median for the assumed range of potential speciation rates (fig. C1). The tempo of the decline is much faster under the model  $M_t$  than under  $M_r$  (fig. 3). Analytic results showed that under various scenarios, the equilibrium average per capita speciation rates are all much lower than the initial rates, that is, the speciation rates are consistently driven toward the lower boundary of the assumed range of potential values (fig. C4).

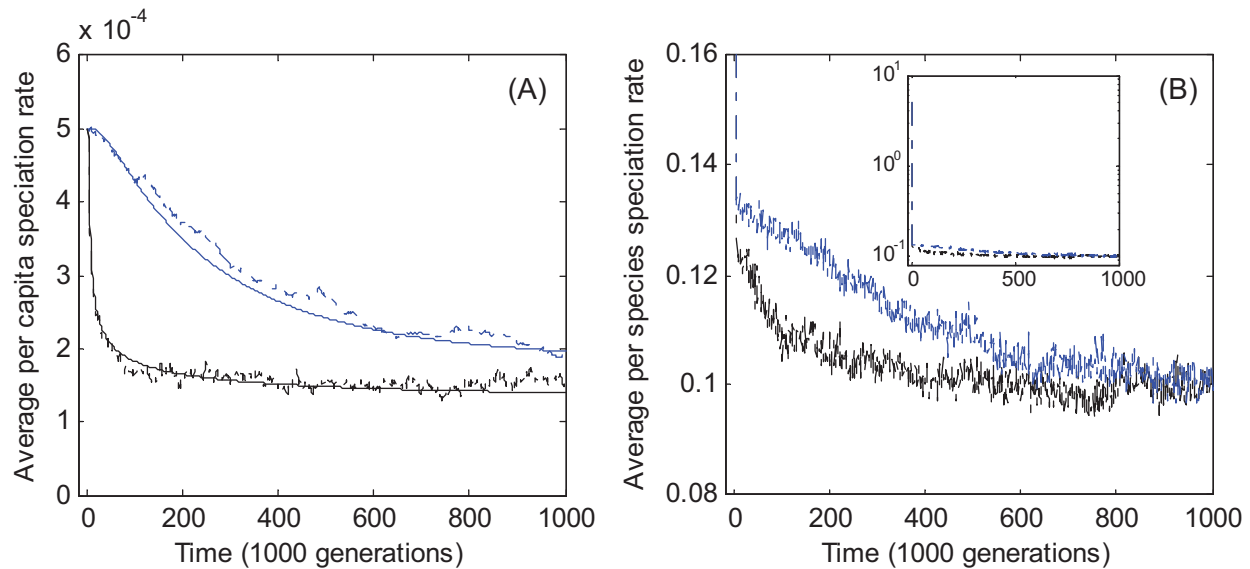
The fission modes of speciation also predict declines in the average per capita and average per species speciation rates (fig. 4). However, these declines are much faster than those under point mutation speciation. The simulations confirmed the analytical result that the decline of the average per capita speciation rate under the fixed fission mode is approximately  $n_0$  times faster than under the point mutation mode (fig. 4A, 4C). They also show that the decline under random fission speciation is more than  $v_{\max}^{-0.5}/4$  times faster than under point mutation speciation (fig. 4E).

Under all the three speciation modes and two scenarios of heritability ( $M_r$  and  $M_t$ ), species with high per capita speciation rates had shorter average life span in the sim-

ulations than those with low rates (fig. 5). This relationship is caused by a negative effect of speciation on a species' ability to resist extinction (see app. E). Speciation places the parent species closer to extinction (population size zero) than it was before speciation. This effect is much larger under the fission modes of speciation, because speciation removes more individuals from the parent during speciation under the fission modes than under the point mutation mode (fig. 5B, 5C). For this same reason, the negative effect of the speciation rate on species life span increases with the number of individuals removed from a parent to form a daughter species under fixed fission speciation (fig. 5B).

## Discussion

The neutral theory of biodiversity bridges from ecological to geologic timescales by incorporating the process of random speciation in a stochastic birth-death model of population dynamics (Hubbell 2001, 2005). This makes NTB a potentially valuable tool for paleontological and phylogenetic studies (Rosindell et al. 2011). Nonetheless, only a few studies have used NTB models to address macroevolutionary issues over geologic timescales (but see Mooers et al. 2007; Davies et al. 2011). Most have focused



**Figure 3:** Temporal trajectories of the average per capita (A) and per species (B) speciation rates under point mutation speciation mode. Black and blue lines represent the results under models  $M_1$  and  $M_2$ , respectively. Parameters are the same as in figure 2. Dash-dotted lines represent the average of 500 simulations (size of the simulated communities:  $J = 10,000$ ). Solid lines in A show analytic solutions from equation (2). In B, the initial sharp decrease (*inset*) is caused by the increase of species diversity, which reached equilibrium before the thousandth generation (fig. C3), but the long-term decline after the thousandth generation (main panel with a truncated Y-axis) is caused by macroevolutionary selection against high speciation rates.

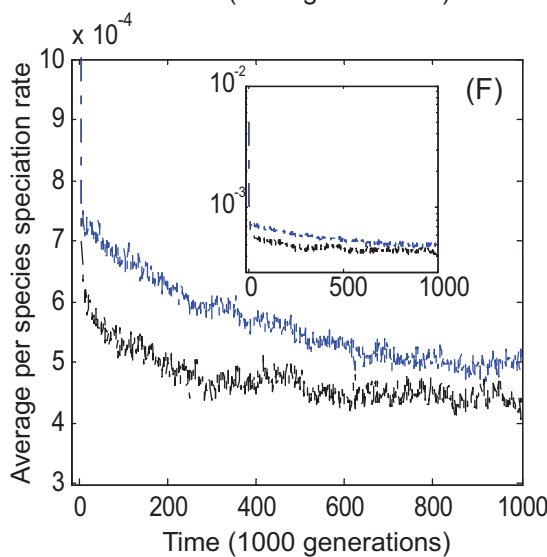
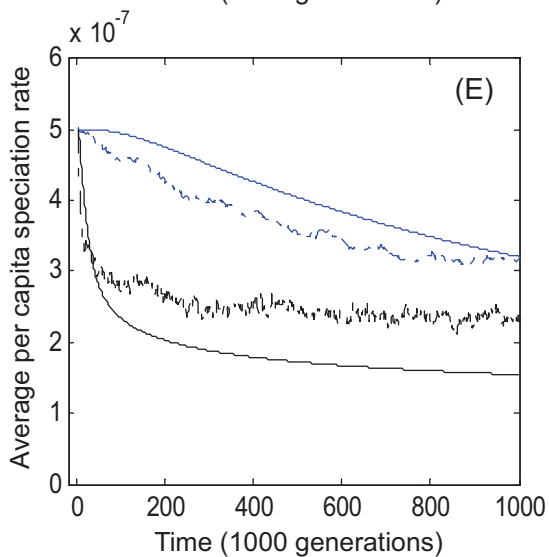
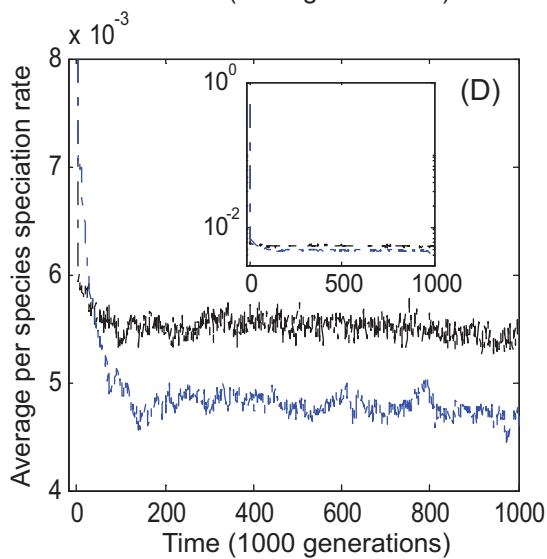
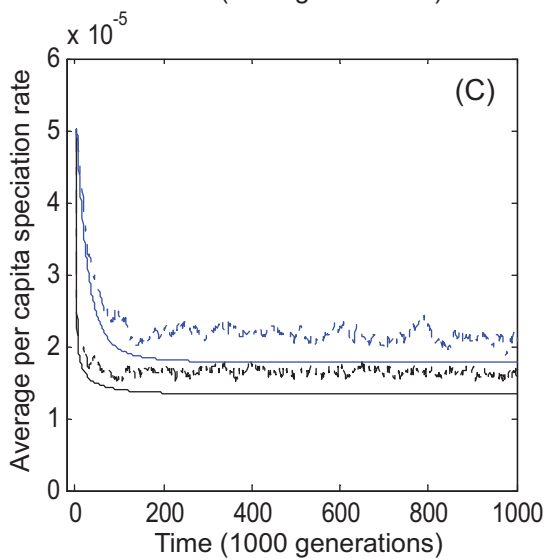
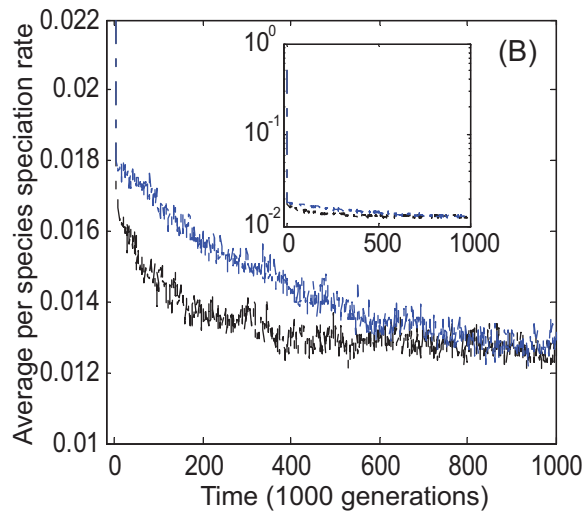
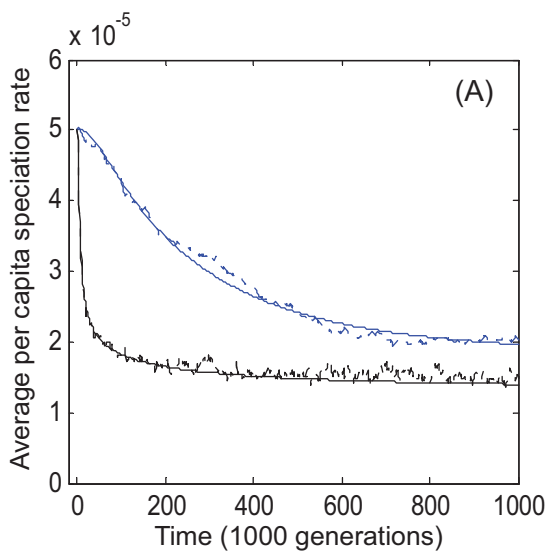
instead mainly on the population dynamics at the ecological timescale (McKane et al. 2000; Azaele et al. 2006; Chisholm 2011). In this article, we examine the macroevolutionary dynamics of neutral communities with the simple NTB model and find that neutral dynamics can predict qualitatively the sudden increase and the subsequent decline in the per-species speciation rate following a mass extinction. Thus, purely neutral ecological dynamics and random speciation at a constant per capita rate may be responsible, at least partly, for some of the examples reported in the literature on macroevolutionary trends following mass extinctions. These trends have previously been attributed to nonneutral ecological processes, such as diversification into empty niches.

However, the simple NTB model cannot predict either observed changes in the total speciation rate (Benton 1995; Levinton 2001), or the long-term decline in per-species speciation rate reported over Phanerozoic time (Sepkoski 1998; Alroy 2008). By extending NTB to include interspecific variation in per capita speciation rates, we show that a low speciation rate helps a species resist extinction, because speciation breaks a single population into two and places the parent species closer to extinction than it was before speciation. The population size reduction that accompanies speciation shortens the expected time for the parent species to drift randomly to extinction (fig. 5). The population dynamic cost of speciation in the model causes

a macroevolutionary selection for reduced speciation rates (both per capita and per-species rates), and consequently causes the average rate of speciation to decline in our simulations. The decline is halted by either: (1) the production of new daughter species with per capita speciation rates higher than the community's average if the speciation rate is incompletely heritable (when the community average rate is near the assumed lower bound), or (2) the assumed lower bound on the per capita speciation rate if the speciation rate is perfectly heritable.

The elevated extinction risk caused by high speciation rate in our  $BD_1$  models thus offers a parsimonious mechanistic explanation for the slow decline in origination rate following the post-mass-extinction rebounds, which is one of the most interesting macroevolutionary patterns (Sepkoski 1998; Phillimore and Price 2009). This same mechanism may also explain the slow declines in the total and per-species extinction rates through the Phanerozoic (Raup and Sepkoski 1982; Van Valen 1984; Foote 2003; Alroy 2008).

The extended NTB model with variable per capita speciation rates cannot, by itself, explain two aspects of the pattern from the fossil record. First, it does not explain why observed slow decreases in the origination rate of new taxa do not always lead to decreased diversity, at least in some clades (Sepkoski 1984, 1998; Benton 1995). Niches may be necessary to explain such cases. Second, the ex-



tended model does not explain the increase in the total rate of origination of new species that immediately follows mass extinction. Nonneutral ecological mechanisms may also be necessary to explain this pattern, such as the presence of empty niches after a mass extinction that are then filled preferentially by taxa with rapid speciation rates. We note, however, that the neutral dynamics of NTB models is robust to the introduction of niches if diversity is sufficiently large (Purvis and Pacala 2005; Chisolm and Pacala 2010). Heuristically, if each niche contains multiple ecologically equivalent species, then species' relative abundances will drift randomly within each niche and so the abundances of any two species from different niches will also drift relative to one another. A similar argument also holds for continuous niches (Purvis and Pacala 2005). The important implication here is that a mass extinction could lead to nonneutral dynamics by reducing the number of species per niche. The subsequent rebound of diversity could then restore approximately neutral dynamics. Thus, niche mechanisms for the macroevolution of increased speciation rates immediately after a mass extinction are not incompatible with neutral mechanisms for the subsequent slow decline in these same rates. An analogous argument applies to an adaptive radiation caused by a new evolutionary innovation.

By incorporating population dynamics in a model of macroevolutionary processes, our  $BD_1$  model successfully overcomes several theoretical difficulties of previous macroevolutionary models. For example, species-based  $BD_s$  models predict an opposite species selection that favors species with high speciation rates (Heard 1996; Mooers et al. 2007), which is the opposite of the observed trend after mass extinctions. In contrast, our model shows how high speciation rates can be selected against. In model  $M_r$ , two forces act against one another: the demographic force that pushes speciation rates down, and the heritability-induced species selection force that favors high speciation rates (as in  $BD_s$  models; Heard 1996). Our analysis shows that the first of these forces is stronger than the second in ecologically neutral models. In model  $M_c$ , the latter force is absent, and as a consequence the demographic force causes a much faster decline in speciation rate. In addition, the fact that drift to extinction is promoted by speciation in our model provides a simple mechanistic explanation for

the positive correlation between speciation and extinction rates, which is an essential assumption in the taxon selection hypothesis (Gilinsky 1994; Sepkoski 1998). Our work also shows how two widely documented patterns of variation in speciation rates—decreases through time within a clade and variability among lineages—may be linked mechanistically (Heard 1996; Sepkoski 1998; Coyne and Orr 2004; Phillimore and Price 2009; Stadler 2011). Previous studies have investigated these two patterns separately but rarely explored their interdependence (but see Gilinsky 1994; Heard 1996).

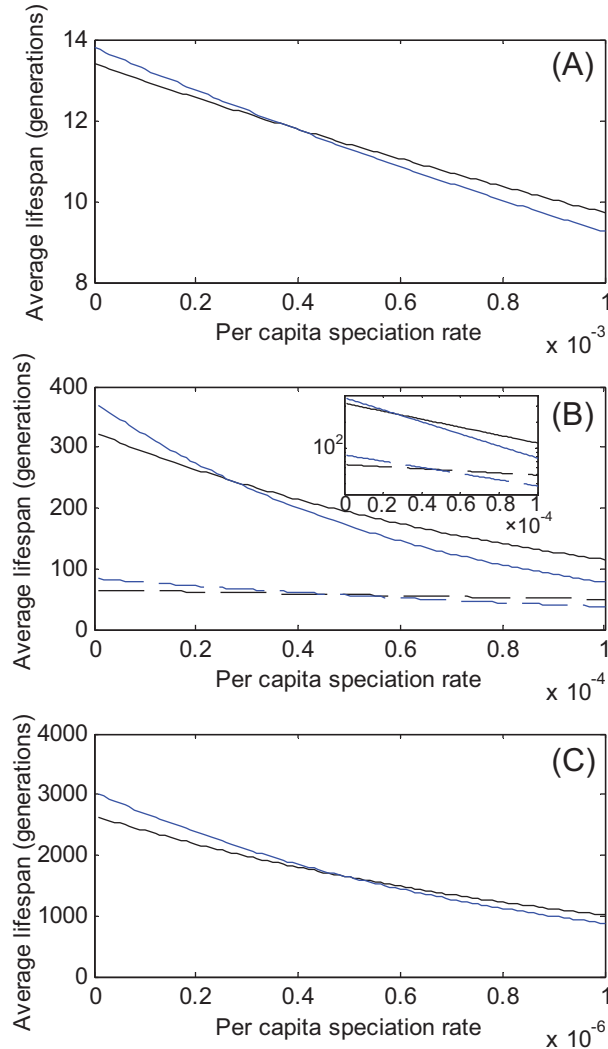
Although the  $BD_1$  model assumes constant total population size of all species taken together, like the original NTB models (Hubbell 2001, 2005), the theoretical prediction of declining speciation rate should be robust to a fluctuating total abundance, for instance, due to environmental and/or demographic stochasticity (Lande et al. 2003; Volkov et al. 2003; Allen and Savage 2007; Houlahan et al. 2007). As the analytic equations (2) and (3) indicate, the dynamics of the average per capita speciation rates are determined by the magnitude and transition probabilities of the speciation rate and are independent of the total community abundance ( $J$ ). Therefore, fluctuations in the community size should have little impact on the predicted decline of the average per capita speciation rate. However, environmental and demographic stochasticity may enlarge the temporal variability in the total origination rate of new species in the community, which is the product of community size and average per capita speciation rate.

An additional problem with the hypothesis offered by our  $BD_1$  model for the Phanerozoic decline in speciation rates is that the declines predicted by the model may be too slow. For example, under the point mutation speciation, if per capita speciation rate is small (e.g., smaller than  $10^{-6}$ ), the average per capita speciation rate would hold nearly constant for  $\sim 100$  million years (fig. C1). However, discovery of cryptic species by the DNA barcoding techniques suggests that new species may have emerged long before they can be recognized morphologically (Bickford et al. 2007). This protracted mode of speciation has also been shown to generate more realistic evolutionary patterns in NTB models (Rosindell et al. 2010; Etienne and Rosindell 2012). Under protracted speciation, the intrinsic rate of speciation can be much higher than con-

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**Figure 4:** Temporal trajectories of the average per capita ( $A, C, E$ ) and per species ( $B, D, F$ ) speciation rate under fixed fission ( $A-D$ ) and random fission ( $E, F$ ) speciation. Black and blue lines represent the results under models  $M_r$  and  $M_c$ , respectively. In all cases, the community starts from one species with initial per capita speciation rate  $v_0 = (v_{\min} + v_{\max})/2$ . Parameters for the fixed fission speciation are  $v_{\min} = 10^{-7}$ ,  $v_{\max} = 10^{-4}$ , and  $L = 2 \times 10^{-5}$ , with initial population size of new species  $n_0 = 10$  ( $A, B$ ) and 100 ( $C, D$ ). Parameters for the random fission speciation ( $E, F$ ) are  $v_{\min} = 10^{-10}$ ,  $v_{\max} = 10^{-6}$ , and  $L = 2 \times 10^{-7}$ . Dash-dotted lines represent the average of 500 simulations (size of the simulated communities:  $J = 10,000$ ), and solid lines show the approximate solutions from equation (3), with  $n_0 = 10$  ( $A$ ),  $n_0 = 100$  ( $C$ ) and  $n_0 = v_{\max}^{0.5}/4 = 250$  ( $E$ ). In  $B, D$ , and  $F$ , the initial sharp decrease (*insets*) is caused by the increase of species diversity, but the subsequent long-term decline (main panels with truncated  $Y$ -axes) is caused by a gradual decline in the average per capita speciation rate.





**Figure 5:** The relationship between average species life span and per capita speciation rate, under the three modes of speciation: point mutation (A), fixed fission (B), and random fission (C). Lines represent the fitted relationships to simulated data using the Gamma family generalized linear model (see app. E, available online). Black and blue lines corresponded to models  $M_1$  and  $M_2$ , respectively. In B, the dashed and solid lines represented the fixed fission mode with initial abundances  $n_0 = 10$  and 100 respectively, and the inset shows species life span on a logarithm scale. See figures 2 and 4 for the values of other parameters.

ventional estimates (Rosindell et al. 2010), which implies a faster decline in the average speciation rate and a shorter period before declines are noticeable. Alternatively, a more reasonable solution may rely on fission modes of speciation, which mimics allopatric speciation, the most common type of species formation (Coyne and Orr 2004). Under fission speciation, the decline of speciation rate after a mass extinction is much faster than under point mutation speciation, due to the large initial abundance of new species (equation [3]). Specifically, the tempo of decline under the random fission speciation with per capita speciation rate of order  $10^{-6}$  can be as fast as that under point mutation speciation with rates of order  $10^{-3}$  (see app. D).

In general, our results demonstrate the value of models that bridge the gap between ecological and geologic time-scales for studies of macroevolutionary phenomena. In our  $BD_1$  model, both the species-level speciation rate and the expected time to extinction are proportional to a species' abundance (Kimura 1983; Hubbell 2001, 2005). This is an assumption for the speciation rate, but a result of neutral ecological dynamics for the time to extinction. Further studies are needed to investigate the macroevolutionary consequences of different relationships between species abundance and macroevolutionary rates, such as in neutral models with constant per-species speciation rates (Etienne et al. 2007; Haegeman and Etienne 2009), and/or density-

dependent individual birth and death rates (He 2005; Volkov et al. 2005). Such abundance-dependent macroevolutionary models may provide novel insights about paleontological and phylogenetic phenomena, and increase our understanding of the interaction between ecological and macroevolutionary processes.

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