

EXPLOSIVE EVOLUTIONARY RADIATIONS: DECREASING SPECIATION OR INCREASING EXTINCTION THROUGH TIME?

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A common pattern in time-calibrated molecular phylogenies is a signal of rapid diversification early in the history of a radiation. Because the net rate of diversification is the difference between speciation and extinction rates, such “explosive-early” diversification could result either from temporally declining speciation rates or from increasing extinction rates through time. Distinguishing between these alternatives is challenging but important, because these processes likely result from different ecological drivers of diversification. Here we develop a method for estimating speciation and extinction rates that vary continuously through time. By applying this approach to real phylogenies with explosive-early diversification and by modeling features of lineage-accumulation curves under both declining speciation and increasing extinction scenarios, we show that a signal of explosive-early diversification in phylogenies of extant taxa cannot result from increasing extinction and can only be explained by temporally declining speciation rates. Moreover, whenever extinction rates are high, “explosive early” patterns become unobservable, because high extinction quickly erases the signature of even large declines in speciation rates. Although extinction may obscure patterns of evolutionary diversification, these results show that decreasing speciation is often distinguishable from increasing extinction in the numerous molecular phylogenies of radiations that retain a preponderance of early lineages.

KEY WORDS: Birth–death model, diversification, macroevolution, phylogeny, speciation, extinction.

A central question in evolutionary biology concerns the extent to which species-level diversification rates vary among lineages and over time. This issue has a venerable history in the paleontological literature (e.g., Simpson 1953; Raup 1985). More recently, the increasing availability of robust molecular phylogenies for clades of extant species has generated a surge of interest in methods to extract information about the tempo and mode of evolutionary diversification from them (Nee et al. 1994a; Paradis 1997; Nee 2006; Rabosky et al. 2007).

Because these statistical tools permit inferences about temporal variation in species-level diversification rates, many studies have applied them in association with time-calibrated phyloge-

nies of extant taxa to characterize rates of lineage accumulation through time during evolutionary radiations. One of the most commonly observed patterns in these studies of diversification rates in extant clades is evidence for bursts of diversification in the early stages of those species-level radiations, followed by declining diversification through time. Such “explosive-early” radiations have been reported from a wide range of taxa and biogeographic settings (e.g., Lovette and Bermingham 1999; Harmon et al. 2003; Shaw et al. 2004; Kozak et al. 2006).

Several alternative ecological hypotheses might explain a pattern of explosive-early diversification reconstructed from a phylogeny of extant species. For example, opportunities for speciation

during adaptive radiation might be inversely related to the number of potentially competing species in existence at any point in time; this model of resource-limited diversification would predict that speciation rates should decline in a density-dependent fashion (Walker and Valentine 1984; Nee et al. 1992; Phillimore and Price 2008). Other models implicitly suggest that extinction rates might increase during the course of evolutionary radiations (e.g., Ricklefs and Cox 1972; Levinton 1979; Hubbell 2000). But because the net rate of diversification is simply the difference between speciation and extinction rates, an increase in the extinction rate could in principle result in precisely the same net diversification rate through time as a decline in the speciation rate. Weir (2006) used a simulation study to suggest that declining speciation was more likely to explain temporal decreases in diversification rates in Neotropical avifaunas, but the generality of this result and underlying mechanisms remain untested.

Here we explore whether evolutionary radiations characterized by explosive-early diversification are more likely to have resulted from declining speciation rates or from increasing extinction rates through time. We develop an analytical framework based on the birth–death process (Kendall 1948; Nee et al. 1994b) that explicitly models speciation and extinction rates that vary continuously through time. We apply these methods to three published phylogenies that have in common a strong pattern of lineage accumulation consistent with early, rapid diversification, and we test whether models specifying constant speciation and time-varying extinction provide a better fit to real data than models of time-varying speciation and constant extinction. We further use simulations of declining diversification through time to contrast features of lineage accumulation curves under scenarios of decreasing speciation and increasing extinction through time.

Methods

MODELING FRAMEWORK

To test whether temporal declines in diversification rates are best explained by changes in speciation or extinction rates, we require a modeling framework for speciation and extinction rates that vary continuously through time. Consider a general birth–death process, where existing lineages give birth to new lineages at a per-lineage rate λ and go extinct with rate μ . The general probability model described below was developed by Nee et al. (1994b); although this framework has not yet been used for inference on time-varying speciation and extinction rates, there is nothing in this model that prohibits λ and μ from varying over time or among lineages.

A simple way to model the growth of a phylogenetic tree through time is to “split” the tree into a collection of daughter branches, with each branch originating at some time t_i and sur-

living to the present day (time T). Here we consider only the reconstructed evolutionary process (Nee et al. 1994b), where all lineages survive to the present; this corresponds to a typical molecular phylogeny, because only those species that have not gone extinct are observed in a phylogeny that includes only extant taxa. Let $\lambda(t)$ and $\mu(t)$ denote time-varying speciation and extinction rates. We are concerned here with temporal variation in lineage diversification rates; although this model can be extended to include among-lineage rate variation, in the model below $\lambda(t)$ and $\mu(t)$ are constant among lineages that exist at time t .

It is convenient to partition the stochastic processes contributing to the likelihood of a phylogenetic tree with N taxa under $\lambda(t)$ and $\mu(t)$ into two components. The first is attributable to speciation events: new lineages arise in a growing clade with a probability proportional to

$$(i - 1)\lambda(t)P(t_i, T), \tag{1}$$

where $P(t_i, T)$ is the probability that a lineage in existence at time t_i will survive to be observed at time T (e.g., the lineage will not go extinct). The $(i - 1)$ term comes from the fact that, immediately prior to the birth of the i ’th lineage at time t_i , the tree contains a total of $(i - 1)$ lineages that could potentially give birth. The second component of the likelihood follows from the observation that each of N lineages survives from some time t_i to T , leaving only a single descendent in the present (itself). It may seem counterintuitive to imagine each lineage leaving only a single progeny lineage, but we are modeling the growth of the phylogenetic tree as a collection of such processes (Fig. 1).

Define $P(t_i, T)$, or the probability that a lineage survives between time t_i and T , as:

$$P(t_i, T) = \left[1 + \int_{t_i}^T \mu(\tau) \exp(\rho(\tau, t_i)) d\tau \right]^{-1} \tag{2}$$

(Kendall 1948), where

$$\rho(\tau, t_i) = \int_{t_i}^{\tau} \{u(s) - \lambda(s)\} ds. \tag{3}$$

When μ and λ are constant through time, μ/λ represents the long-term probability that a lineage goes extinct (e.g., Raup 1985), and it is true that

$$\lim_{T \rightarrow \infty} P(t_i, T) = \mu/\lambda. \tag{4}$$

To calculate the probability that each lineage i leaves a single progeny (itself) on the interval (t_i, T) , we note that the number of progeny lineages under the birth–death process follows a geometric distribution. The probability that a birth–death process beginning with a single lineage will result in k surviving lineages after some time T is given by $(1 - u)^k$, where $1 - u$ is the parameter of the geometric distribution of progeny lineages (Nee et al.

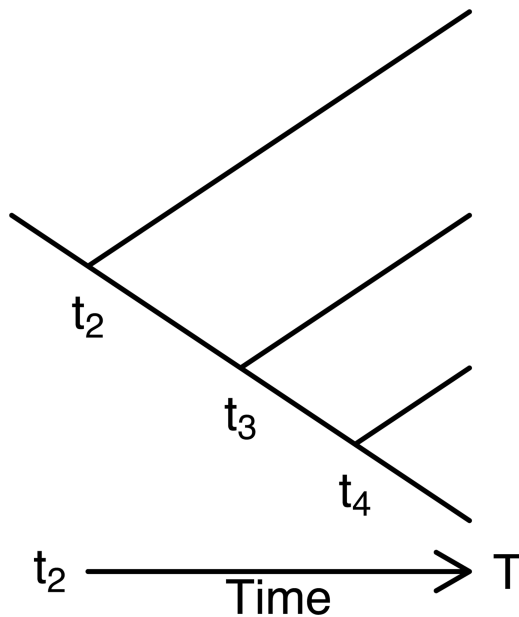


Figure 1. Reconstructed phylogenetic tree illustrating parameters described in text. Time is measured from the root to the present (time T), with each t_i corresponding to the speciation time of the i 'th lineage. By definition, a clade originates with the birth of a second lineage at time t_2 ; note that the two basal lineages that define the clade persist from time t_2 to T .

1994b). We denote the probability that lineage i leaves a single progeny in the present as ξ_i , where

$$\xi_i = P(t_i, T) \exp[\rho(T, t_i)]. \quad (5)$$

Combining equations (1) and (5), we obtain the likelihood for N lineages

$$L = (N - 1)! \prod_{i=3}^N \{\lambda(t_i) P(t_i, T)\} \prod_{i=3}^N \{\xi_i\} \{\xi_2^2\} \quad (6)$$

which is identical to Nee et al. (1994b; eq. 20). Note that the t_i 's are simply the speciation times (Fig. 1). Equation (6) considers only $N - 2$ speciation events, because the first two speciation events must have occurred; if they had not, no phylogenetic tree would exist to be observed (Nee et al. 1994b). The ξ_2^2 term in equation (6) corresponds to these two basal branches. The likelihood function (eq. 6) frequently results in positive log-likelihood values; this occurs because the $(i - 1) \lambda(t) P(t_i, T)$ component of the likelihood is not normalized and is merely proportional to the actual probability density.

MODELS FOR DECLINING DIVERSIFICATION RATES

Our general approach is to ask whether the pattern of lineage accumulation through time in a molecular phylogeny is best explained by a model with constant speciation and time-varying extinction, or by a model with constant extinction and time-varying speciation. The first step of the process is to choose appropriate models

for $\lambda(t)$ and $\mu(t)$. We used a simple exponential model, under which the time-varying speciation rate is given by

$$\lambda(t) = \lambda_0 \exp(-kt), \quad (7)$$

where λ_0 is the initial speciation rate and k specifies the magnitude of the rate decline through time ($0 \leq k < \infty$). When $k = 0$, the speciation rate is constant through time. The time-varying extinction rate was modeled as

$$\mu(t) = \mu_0 (1 - \exp[-zt]), \quad (8)$$

where μ_0 is the asymptote of the increasing extinction rate through time and z controls the steepness of the increase in extinction with respect to time ($0 < z < \infty$). When z is very large, the extinction rate is a constant μ_0 through time. These models are flexible and can accommodate a range of declining diversification scenarios.

We assumed that declining net diversification rates through time could result from three general processes (1) declining speciation through time but constant extinction (a three-parameter model: λ_0 , k , and μ); (2) increasing extinction through time, but constant speciation (three parameters: μ_0 , z , and λ); and (iii) declining speciation rates and increasing extinction rates through time (four parameters: λ_0 , k , μ_0 , and z). For clarity, we refer to these models as SPVAR (time-varying speciation only), EXVAR (time-varying extinction only), and BOTHVAR (both speciation and extinction vary through time). Thus, for the SPVAR model, the net diversification rate $r(t)$ is given by

$$r(t) = \lambda_0 \exp(-kt) - \mu_0 \quad (9)$$

and for the EXVAR model,

$$r(t) = \lambda_0 - \mu_0 (1 - \exp[-zt]) \quad (10)$$

and for BOTHVAR,

$$r(t) = \lambda_0 \exp(-kt) - \mu_0 (1 - \exp[-zt]). \quad (11)$$

We constructed likelihood functions for SPVAR, EXVAR, and BOTHVAR models by finding analytical solutions to equation (3) and substituting the relevant expression into equations (2) and (6). For nonlinear models of speciation and extinction, there is generally no analytical solution to the integral in equation (2); we performed the required numerical integrations using the QUADPACK-derived routine (Piessens et al. 1983) as implemented in the function "integrate" for the R programming environment (<http://cran.r-project.org/>). Models were fitted to phylogenetic data using a box-constrained derivation of the BFGS quasi-Newton method (Byrd et al. 1995). This enabled us to enforce constraints on parameters to meet assumptions of the model, specifically the fact that extinction rates cannot exceed speciation

rates. Optimization was performed in R using the function “optim” with the “L-BFGS-U” method. Because optimization of the likelihood function can fail when multiple optima are present, we repeated all optimization procedures 100 times with random starting parameter values. All source code for numerical fitting of SPVAR, EXVAR, and BOTHVAR models has been placed in the R package LASER (Rabosky 2006a).

APPLICATION TO DATA

To determine whether patterns of diversification during explosive-early radiations are best explained by changes in speciation or extinction rates, we applied the method to three published phylogenies: (1) Australian lizards in the family Agamidae (Harmon et al. 2003); (2) North American wood-warblers in the genus *Dendroica* (Lovette and Bermingham 1999); and (3) Australo-Papuan pythons (Rawlings et al. 2008). These three radiations all show a phylogenetic pattern of explosive-early diversification, followed by declining diversification rates through time. We selected these studies because the phylogenetic trees used in each case are 93+% complete at the species level, reducing the risk of detecting spurious declines in diversification rates due to incomplete taxon sampling (Pybus and Harvey 2000), and because conclusions about declining diversification rates were previously inferred in each case by at least two different methods (e.g., Pybus and Harvey 2000; Rabosky 2006b).

For each group, we obtained the ultrametric trees used to produce the lineage-through-time (LTT) plots that appeared in the original papers. All data were rescaled such that the basal divergence occurred 1.0 time units before the present, and we then fitted the three rate-variable diversification models (SPVAR, EXVAR, BOTHVAR) to each tree. For comparison with the constant-rate diversification process, we also fitted each tree with a simple two-parameter birth–death model, where $\lambda(t) = \lambda$ and $\mu(t) = \mu$. We could not use the likelihood-ratio test to compare models because the SPVAR and EXVAR models are not nested; rather, we compared model fits using the Akaike Information Criterion (AIC).

QUALITATIVE FEATURES OF LINEAGE ACCUMULATION CURVES

We also employed simulations to investigate features of lineage accumulation curves when net diversification rates decline through time. We simulated phylogenetic trees under a model of temporally decreasing diversification, where the decline was caused by either decreasing speciation rates or increasing extinction rates. Most previous studies that have simulated time-varying diversification processes have used discrete-time phylogenetic simulation algorithms (e.g., Paradis 1997; Rabosky 2006b), in which phylogenetic trees are generated by iterating over a series of time steps such that each lineage has a probability of giving birth or going extinct each time step. Because the discrete-time approach is merely

an approximation of the continuous-time diversification process, we implemented a simulation procedure that enables phylogenies to be simulated in continuous time with time-varying diversification parameters.

For a given diversification model (e.g., SPVAR) and magnitude of rate change (e.g., a 10-fold reduction in the net diversification rate through time), we found parameters that would—on average—result in a target number of lineages after $t = 1.0$ time units. We then divided the total simulation time into 50 intervals of $t = 0.02$ time units and calculated mean values of λ and μ for each interval given the overall diversification parameters λ_0 , k , μ_0 , and z . Each simulation was initiated with two lineages, which had parameters λ_1 and μ_1 on the first time interval; after $t = 0.02$ time units, parameters were updated to λ_2 and μ_2 and the simulation was continued to the end of the second time interval (overall elapsed time of 0.04 time units). These sequential parameter updates were continued until the end of the simulation. Thus, although we used a discrete approximation to model and track variation in λ and μ , the underlying simulation occurred in continuous time. All phylogenetic simulation was conducted using a modified version of the birth–death tree simulation algorithm from the Geiger package for R (Harmon et al. 2008).

We simulated phylogenies undergoing fivefold and 15-fold declines in net diversification rates through time assuming the following diversification models: (1) declining speciation through time, but zero extinction; (2) declining speciation through time, with high (constant) background extinction; and (3) increasing extinction through time, with constant speciation. For each scenario, we found λ_0 , k , μ_0 , and z parameters that would result in an expected number of 80 lineages per simulation using equations (7–11) (Table 1). We then performed 1000 simulations under each diversification model; to reduce any potentially confounding effects of very small or very large phylogenies (e.g., Price 2008), we retained only those simulations that contained between 40 and 120 surviving lineages at the end of the simulation. Parameters used for each diversification scenario are given in Table 1, and

Table 1. Parameters used for simulating phylogenies undergoing temporal declines in the net diversification rate. Simulations were conducted for 1.0 time units, with parameter updates every 0.02 time units. Parameters were chosen to yield an average of 80 surviving lineages at the end of the simulation.

Model	Rate decrease	λ_0	k	μ_0	z
SPVAR	5×	7.5	1.64	0	–
SPVAR	15×	10.9	2.77	0	–
SPVAR	5×	9.9	0.83	3	–
SPVAR	15×	11.6	1.2	3	–
EXVAR	5×	7.65	–	7.5	1.73
EXVAR	15×	11.475	–	11.25	3.12

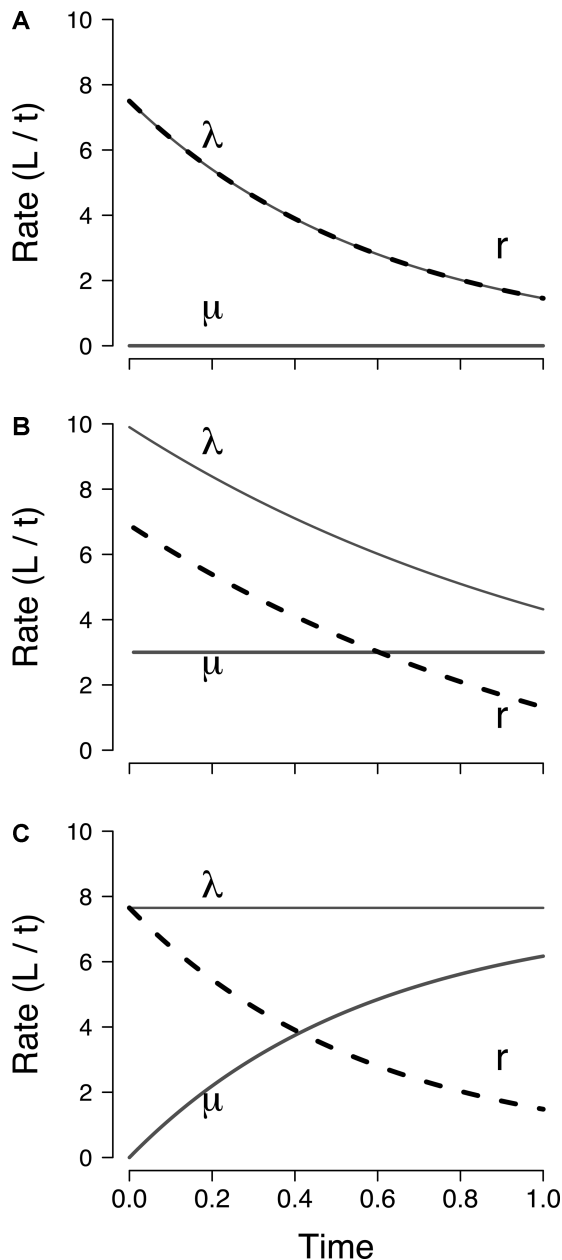


Figure 2. Models used to simulate phylogenies undergoing five-fold decline in net diversification rate (r ; dashed line) attributable to (A) decreasing speciation rate (λ) and with an extinction rate (μ) equal to zero; (B) decreasing speciation, with extinction constant but greater than zero; and (C) speciation constant and extinction increasing through time. Rate through time curves are based on parameters given in Table 1 and were selected to result in a mean of 80 surviving lineages after 1.0 time units.

diversification curves illustrating temporal changes in λ , μ , and r under the simulation model are shown in Figure 2.

To test the extent to which temporal declines in net diversification rates can be inferred from phylogenies generated under time-varying speciation and extinction models, we computed the γ -statistic (Pybus and Harvey 2000) for each batch of simulated

phylogenies. This statistic provides a convenient summary of the distribution of internode distances in a phylogenetic tree; under a constant rate diversification process with $\mu = 0$, γ follows a standard normal distribution. A constant rate diversification process with $\mu > 0$ will result in $\gamma > 0$. However, only temporal declines in diversification rates can result in $\gamma < 0$ (Pybus and Harvey 2000).

Results

RECONSTRUCTED SPECIATION AND EXTINCTION RATES IN REAL PHYLOGENIES

The three model phylogenies show pronounced evidence for temporally declining diversification rates. Calculated γ -statistics for each phylogeny are significantly less than zero, and thereby strongly reject both constant-rate diversification processes and temporally increasing diversification rates (agamids: $\gamma = -4.50$, $P < 0.001$; warblers: $\gamma = -4.20$, $P < 0.001$; pythons: $\gamma = -3.15$, $P < 0.001$). In each case, the SPVAR model fit the observed pattern of speciation much better than both the constant rate birth–death model and the EXVAR model (Table 2). More surprisingly, even the constant rate birth–death model consistently fit the data better than the EXVAR model. Despite a pronounced decline in the speciation rate inferred under the SPVAR model (Table 2; $\Delta\lambda$), the change in extinction through time under the EXVAR model (Table 2; $\Delta\mu$) was zero for all three datasets, indicating that the best-fit parameterization of this model does not differ from a constant rate birth–death model. This result shows that the “explosive early” pattern seen in these topologies cannot be explained by an increase in extinction rates in the more recent period of the radiations.

Likelihoods under the four-parameter BOTHVAR model were identical to those under the three-parameter SPVAR model (Table 2). This is possible because the SPVAR model is simply a special case of the BOTHVAR model with constant extinction through time; thus, if no change in extinction is inferred under BOTHVAR, likelihoods should be identical to those under SPVAR. Reconstructed speciation and extinction through time curves under the BOTHVAR model suggest that speciation rates in agamids, warblers, and pythons have decreased markedly during the course of these radiations, with rates in warblers undergoing the most severe decline (Fig. 3). These curves are virtually indistinguishable from those inferred under the SPVAR model and specify extinction rates that are at most only marginally greater than 0. The only (minor) exception occurs in the warblers, where we found a trivial increase in the extinction rate through time ($\Delta\mu = 0.23$, but compare with $\Delta\lambda = -8.87$); for the warblers as for the other clades, the BOTHVAR model provides poorer fit than does the SPVAR model ($\Delta\text{AIC} = 2.0$; Table 2). Because SPVAR and BOTHVAR differ by only a single parameter, and because SPVAR

Table 2. Results of fitting constant-rate (birth-death) and variable-rate (SPVAR, EXVAR, BOTHVAR) models to phylogenies of agamid lizards, wood-warblers, and pythons. Maximum log-likelihoods and Δ AIC scores (parentheses) are shown for each model, where the lowest Δ AIC indicates the best-fit model. For each phylogeny, the SPVAR model provided the best fit to the data. $\Delta\lambda$ and $\Delta\mu$ indicate net change in speciation and extinction rates between time of the basal divergence and present day under SPVAR and EXVAR models, respectively.

Data	Birth-death	SPVAR	EXVAR	BOTHVAR	$\Delta\lambda$	$\Delta\mu$
Agamids	207.9 (17.6)	217.7 (0)	207.9 (19.6)	217.7 (2.0)	-7.89	0
Warblers	42.1 (19.6)	52.9 (0)	42.1 (21.6)	52.9 (2.0)	-9.3	0
Pythons	49.2 (6.3)	53.3 (0)	49.2 (8.3)	53.3 (2.0)	-7.53	0

is a special case of BOTHVAR, it is not possible to obtain Δ AIC in favor of SPVAR greater than the observed value of 2.0. These patterns suggest that the changes in net diversification rates through time in these groups have been mediated almost entirely by declining speciation rates and not by increasing extinction rates.

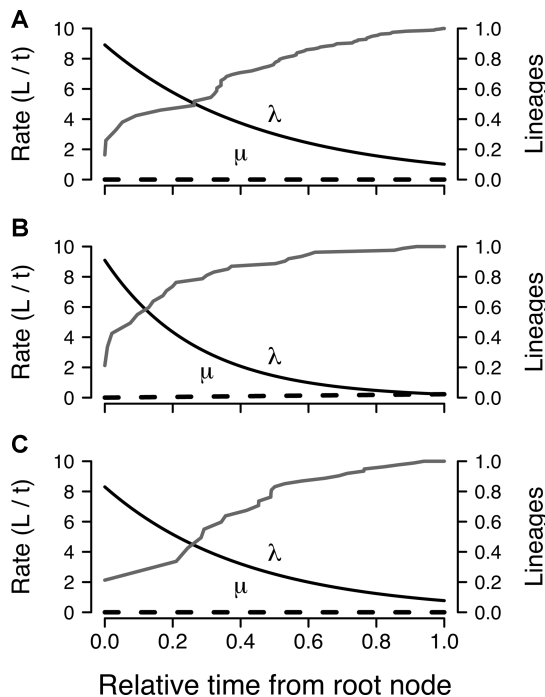


Figure 3. Maximum-likelihood estimates of speciation rates (λ , solid line, decreasing) and extinction rates (μ , dashed line) under the BOTHVAR model for three phylogenies discussed in text: (A) Australian agamid lizards, (B) North American wood-warblers, and (C) Australo-Papuan pythons. The corresponding log-lineage through time curves (solid line, increasing) are included in each plot. Phylogenies were taken from original sources and rescaled to a basal divergence of 1.0 time units before the present. Rates are given in units of lineages per time unit. In each phylogeny, the extinction rate is inferred to have undergone minimal or no increase through time; in contrast, speciation rates consistently show a large decline. Speciation rates declined most rapidly in wood-warblers (B), as assessed by the slope of the speciation rate curve.

SPECIATION AND EXTINCTION RATE SIMULATIONS

Our simulations show that patterns of lineage accumulation through time during explosive-early radiations vary dramatically depending on whether declining diversification rates are a function of decreasing speciation or increasing extinction rates (Fig. 4). When speciation rates decrease through time, the number of surviving lineages in existence at any point in time is greater than the expected number of lineages under a constant rate diversification process (Fig. 4A, B). However, this excess of lineages is replaced by a sigmoidal relationship that much more closely mimics the null pattern when comparable changes in the net diversification rate are driven by increasing extinction rates (Fig. 4C, D). Under both high extinction scenarios, a modest excess in the number of lineages during the earliest stages of a radiation switches to a modest paucity of lineages later in the radiation, where the LTT curve for more recent divergences shows the upturn thought to be characteristic of increasing diversification rates through time or high relative extinction rates (Nee et al. 1994a; Rabosky 2006b). This sigmoidal pattern in the simulated LTT plots is especially striking when large increases in net diversification rates are driven solely by increasing extinction rates through time (e.g., Fig. 4D).

When phylogenies are simulated under a model of declining speciation rates with no extinction, the γ -statistic gives the expected result: larger declines in speciation rates result in lower γ values (Fig. 5A,B). However, when speciation rates decline under high but constant extinction, the signature of explosive-early diversification is absent (Fig. 5C,D). For a modest fivefold decrease in the speciation rate, γ is significantly greater than zero when extinction is relatively high ($t = 6.155$; $df = 999$; $P < 0.001$). Under a 15-fold decline in the net diversification rate with high but constant extinction, the majority of the distribution of γ lies within the 95% confidence interval for a constant rate diversification process with no extinction (Fig. 5D). No signature of declining net diversification rates can be detected with the γ -statistic when the rate decrease is attributable to increasing extinction through time (Fig. 5E,F); this is a particularly striking pattern when compared to identical changes in net diversification rates attributable to declining speciation only (Fig. 5A,B).

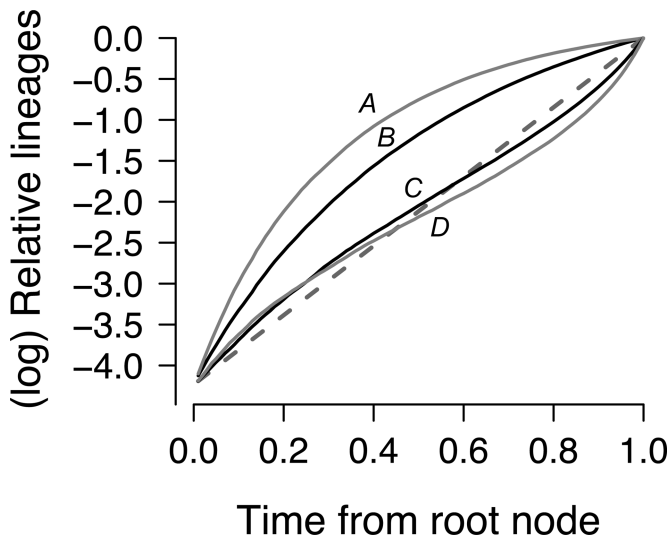


Figure 4. Mean log-lineage through time curves for phylogenies simulated under alternative diversification scenarios. (A) 15-fold decrease in net diversification rate (r) mediated by declining speciation rates, with no extinction; (B) Fivefold decrease in r mediated by declining speciation rates, with no extinction; (C) Fivefold decrease in r mediated by increasing extinction through time, with constant speciation; (D) 15-fold decrease in r mediated by increasing extinction, with constant speciation. Curves are based on 1000 simulations using diversification parameters given in Table 1 and were rescaled to a maximum of 1.0 lineages. Despite a large real decline in their net diversification rate, phylogenies generated under increasing extinction (C and D) show an characteristic upturn in the number of lineages toward the present, a pattern that is typically interpreted as stemming from increasing diversification through time or from high but constant relative extinction rates.

Discussion

We developed and explored a framework for modeling time-varying speciation and extinction rates and for testing whether the pattern of explosive-early diversification seen in many evolutionary radiations is best explained by declining speciation rates or by increasing extinction rates. Although these competing models can result in identical net diversification rates through time, our results indicate that only declining speciation rates leave a signature of rapid lineage accumulation early in the history of radiations that can be inferred from molecular phylogenies that include only extant taxa. We analyzed three representative phylogenies known to show this pattern of rapid, early lineage accumulation and found that a model specifying temporally declining speciation rates provided a much better fit than a model with increasing extinction rates. More surprisingly, the model specifying increasing extinction rates through time failed to fit the data better than a simple constant rate birth–death model (Table 2). In each case, maximum-likelihood parameter estimates under the variable extinction model specified no change in the extinction rate through time.

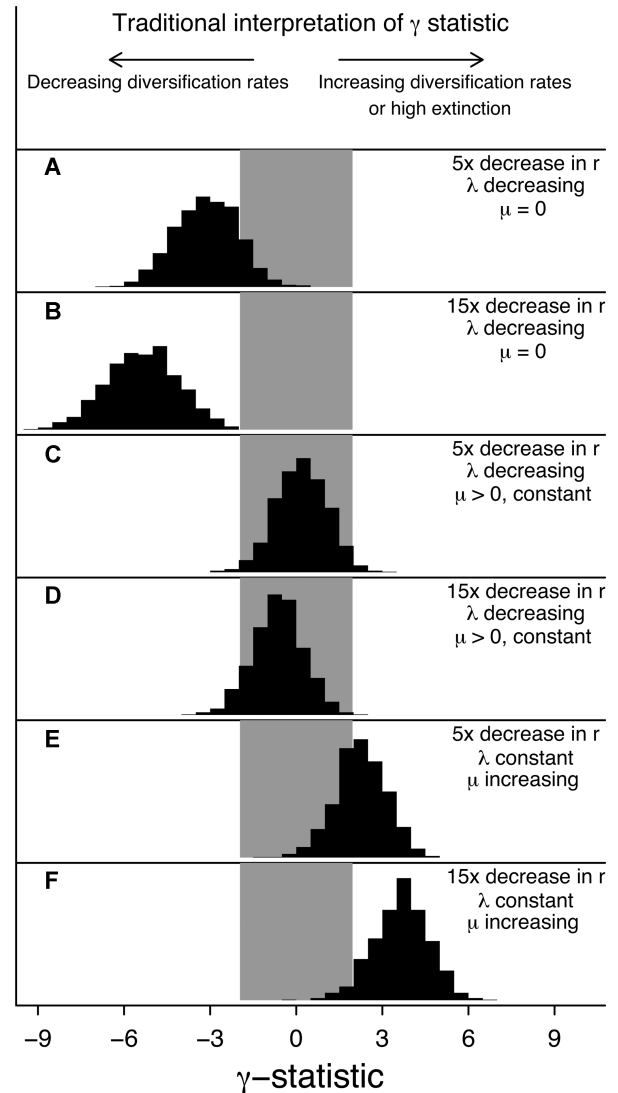


Figure 5. Distribution of γ statistic for phylogenies simulated with identical net diversification rates (r) but with different speciation (λ) and extinction (μ) parameterization. Gray region represents 95% confidence interval on the null hypothesis of constant diversification through time under the pure-birth ($\mu = 0$) model. (A) Fivefold and (B) 15-fold declines in r mediated by a decline in the speciation rate, with zero extinction. (C) Fivefold and (D) 15-fold declines in r mediated by declining speciation, but with high and constant rates of background extinction. (E) Fivefold and (F) 15-fold declines in r mediated by increasing extinction and constant speciation rates.

Why do models specifying temporal increases in extinction rates fail to fit these lineage accumulation curves better than a simple constant rate birth–death model? Our analyses of simulated datasets with temporally declining net diversification rates provide a ready explanation for this phenomenon. Although both declining speciation and increasing extinction can yield identical net diversification rates through time, patterns of lineage accumulation vary dramatically between these competing

models of diversification. When speciation rates decline through time with low background extinction, LTT plots reveal a rapid rise in the number of lineages early in the history of the radiation (Fig. 4A, 4B). This is the LTT relationship expected to result from declining diversification through time (Nee et al. 1992; Wollenberg et al. 1996; Pybus and Harvey 2000), and it is the pattern seen in the phylogenies for the three real taxonomic groups we analyzed as representatives of this common phenomenon. As expected, our simulations also show that the γ statistic becomes increasingly negative as the speciation rate decline becomes more severe (Fig. 5A, 5B).

However, when changes in the net diversification rate are mediated solely by increasing extinction rates through time, reconstructed LTT curves bear little trace of the high diversification rates that were present in the early stages of a radiation (Fig. 4C, 4D). Distributions of γ for such phylogenies indicate that the relative waiting times between successive speciation events (as inferred from the topology that includes only extant taxa) retain no signature of declining net diversification rates through time (Fig. 5E, 5F). When phylogenies are simulated under the EXVAR model, we found that the largest declines in diversification rates yield the largest values of γ (Fig. 5F); such positive values of γ are traditionally interpreted as consistent with increasing diversification through time or high extinction (e.g., Barraclough and Vogler 2002; Linder et al. 2003). These high γ values under high extinction are almost certainly due to the “pull of the present” (Nee et al. 1994a,b), whereby high relative extinction rates—the ratio of extinction to speciation—create an apparent excess of recently diverged lineages in reconstructed phylogenies. This phenomenon has been discussed previously as a potentially confounding issue in diversification analyses (Nee 2001; Rabosky 2006b), because high relative extinction rates can create the spurious impression of increasing diversification through time, even when rates have not changed. Here we find that this effect is strong enough to overcome even massive declines in net diversification rate, potentially leading researchers to infer a temporal increase in net diversification rates in situations in which net diversification is actually declining via increasing extinction.

These results imply that traditional interpretations of LTT plots and associated test statistics may be naive if the potential role of extinction is neglected. An apparent excess of recently diverged lineages in LTT plots is typically interpreted as consistent with increasing diversification through time or high relative extinction rates (Barraclough and Vogler 2002; Turgeon et al. 2005; Rabosky 2006b; Roelants et al. 2007). Our results indicate that declining net diversification through time could yield similar patterns of lineage accumulation in reconstructed phylogenies, if the decline is driven by increasing extinction rates.

We also found that high but constant extinction rates erode the signature of explosive-early speciation. We expected to ob-

serve some reduction in our ability to detect temporally declining speciation under high background extinction, as the “pull of the present” would partially offset the rapid rise in lineages at the start of the radiation. However, we were unprepared for the observation that the distribution of γ from even a 15-fold decline in the net diversification rate was virtually indistinguishable from a constant rate diversification process (Fig. 5C, D) under high but constant extinction rates. This result suggests that, when background extinction rates have been high, even large declines in the rate of speciation through time will be difficult to detect using phylogenies of extant taxa only.

The power of extinction, whether constant or variable, to influence LTT plot-based inferences about diversification rates raises an important question: how often will real-world extinction rates be high relative to speciation rates? Evidence from the fossil record supports the view that relative extinction rates are generally high (e.g., Stanley 1979; Stanley et al. 1988; Gilinsky 1994; Newman and Sibani 1999), and we are unaware of any evidence that extant clades have diversified in the absence of extinction. In the case of mammals, for example, Alroy (1996) found mean per-genus and per-lineage relative extinction rates of 0.90 and 0.91, respectively, across 55 one million year intervals during the Cenozoic. In Gilinsky’s (1994) tabulation of familial origination and extinction rates in marine invertebrates, nearly two-thirds of all orders have had relative extinction rates in excess of 0.8 (91/137). This raises a conundrum: the fossil record suggests that real clades will often evolve under conditions that should make it difficult to ever detect temporally declining speciation rates from LTT analyses of extant species, yet a large number of empirical studies have documented exactly that pattern across a diverse range of taxonomic groups. How can it be that so many radiations provide strong LTT evidence for explosive-early diversification?

We suggest two possible solutions to this seemingly paradoxical observation. The first is simply that fossil-derived relative extinction rates do not apply to phylogenies of extant taxa. This could be the case if relative extinction rates are highly conserved among closely related taxa (e.g., Heard and Mooers 2000). For example, mammals are characterized by high relative extinction rates (Alroy 1996), but it is not clear whether these overall rates apply to the subset of mammalian lineages that have actually survived to the present and are hence available for LTT-based comparisons. A number of mammalian subclades have gone extinct entirely (Bininda-Emonds et al. 2007), and relative extinction rates for at least some clades that survived to the present are somewhat lower than Alroy’s overall (1996) estimate (Munoz-Duran 2002).

A second possibility is that explosive-early diversification is often an artifact of methodological biases stemming from taxon sampling issues or the methodologies used to generate phylogenetic trees for LTT comparisons. Current LTT approaches assume that extant taxa of equivalent biological rank (e.g., “species”) are

comprehensively sampled, and that the temporal distribution of nodes (i.e., branch lengths) in their phylogeny is not biased with respect to age. Incomplete taxon sampling will result in a spurious decline in speciation rates as inferred from reconstructed phylogenies (Nee et al. 1994a; Pybus and Harvey 2000). We recognize that many clades will contain unrecognized or unsampled lineages whose exclusion could bias diversification analyses; this may be a particularly prevalent issue in clades in which divergent phylogeographic lineages are not recognized and included as incipient species. Failure to use an appropriate model of sequence evolution may also lead to disproportionate compression of early branches in phylogenetic trees (Revell et al. 2005), thus creating the impression of decreasing speciation through time. Similar problems may also be associated with different algorithms for constructing ultrametric trees (e.g., Ruber and Zardoya 2005). However, these are methodological artifacts of the phylogeny reconstruction process, not of the LTT approaches applied to those phylogenies.

The analytical framework described here for modeling speciation and extinction rates that vary continuously through time should be applicable to a range of problems involving temporal and among-lineage variation in diversification rates. The basic model for time-varying diversification rates (eqs. 2–6) can be modified to allow speciation and extinction probabilities to vary among lineages, perhaps as a function of species trait values (e.g., Paradis 2005). The advantages of using a general framework based on the birth–death process are twofold. First, in contrast to simple parametric and nonparametric diversification test statistics (Wollenberg et al. 1996; Paradis 1998; Pybus and Harvey 2000), our model-fitting approach provides biologically meaningful parameter estimates and—as demonstrated here—can be used to infer changes in both speciation and extinction rates through time. This distinguishes our approach from survival analysis (Paradis 1997), which can accommodate continuous-time variation in speciation rates but is limited by its explicit assumption of zero extinction (Felsenstein 2004).

A second advantage of the present approach is that it provides researchers the power to address specific macroevolutionary questions with a large range of biologically relevant diversification models. There is nothing special about the models for time-varying diversification we selected for this study; we chose them for their simplicity (3 or 4 parameters), flexibility (we could model nonlinear changes in speciation and extinction rates), and because they permitted us to address our focal question. The computational tools for numerical integration and optimization available through R, MATLAB, and other analysis platforms make it possible to fit diversification models that are more complex than those discussed in the present article. Of course, it is always the case that models can only approximate evolutionary processes, and matching a model to a particular question is not a trivial undertaking (Bolker 2008). Knowledge of dubious quality is gained when one poorly

formulated model is found to fit the data better than another poorly formulated model.

In summary, we found that explosive-early radiations, as inferred from molecular phylogenies of extant taxa, can only be explained by temporal declines in speciation rates and not by increasing extinction rates through time. Some theoretical work suggests that the extinction rates should increase through time during evolutionary radiations as a function of mean population sizes or per-capita resource availability (e.g., Levinton 1979; Hubbell 2000). If this occurs, it is unlikely to leave a signature of early, rapid diversification in molecular phylogenies. To the extent that patterns of lineage accumulation observed in empirical datasets are not artifacts of biased branch-length reconstruction or incomplete taxon sampling, our results suggest that many clades appear to undergo rapid diversification early in their history because speciation, but not extinction, rates have changed over the histories of those groups.

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