

Primary Controls on Species Richness in Higher Taxa

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Abstract.—The disparity in species richness across the tree of life is one of the most striking and pervasive features of biological diversity. Some groups are exceptionally diverse, whereas many other groups are species poor. Differences in diversity among groups are frequently assumed to result from primary control by differential rates of net diversification. However, a major alternative explanation is that ecological and other factors exert primary control on clade diversity, such that apparent variation in net diversification rates is a secondary consequence of ecological limits on clade growth. Here, I consider a likelihood framework for distinguishing between these competing hypotheses. I incorporate hierarchical modeling to explicitly relax assumptions about the constancy of diversification rates across clades, and I propose several statistics for a posteriori evaluation of model adequacy. I apply the framework to a recent dated phylogeny of ants. My results reject the hypothesis that net diversification rates exert primary control on species richness in this group and demonstrate that clade diversity is better explained by total time-integrated speciation. These results further suggest that it may not be possible to estimate meaningful speciation and extinction rates from higher-level phylogenies of extant taxa only. [Adaptive radiation; birth–death model; extinction; macroevolution; speciation; species richness.]

Why do some groups have so many species, and why do many other groups have so few? This question has intrigued evolutionary biologists and ecologists for decades, yet there is little consensus on the primary determinants of species richness in clades. Nonetheless, the ever-increasing availability of time-calibrated molecular phylogenies provides a rich source of information with which to test hypotheses about differential diversification across the tree of life (e.g., Mooers and Heard 1997; Moore et al. 2004; Ricklefs 2007), raising the possibility that we will soon converge on general explanations for the variation in species richness among clades and regions. Progress toward this goal has been facilitated by the development of sophisticated methods for inferring rates of speciation and extinction from phylogenetic data (Paradis 2005; Maddison et al. 2007; Freckleton et al. 2008; FitzJohn et al. 2009).

Hypotheses to explain differential species richness encompass a broad range of mechanisms (Heard and Hauser 1995). Some lineages appear to possess key traits that promote speciation (Jablonski 2008; Rabosky and McCune 2010), such as those associated with pollinator specificity in plants (Hodges and Arnold 1995; Sargent 2004) and sexual selection in animals (Coyne and Orr 2004; Mank 2007; Seddon et al. 2008). Alternatively, some lineages might have lower extinction rates than others (Purvis 2008; Vamوسي and Wilson 2008; Roy et al. 2009), presumably associated with traits like geographic range size (Jablonski and Hunt 2006; Cooper et al. 2008). In addition to such lineage-specific traits, extrinsic environmental factors may also modulate speciation and extinction rates. For example, variation in diversification rates has been linked to climate (Weir and Schluter 2007), environmental energy (Davies et al. 2005), as well as dispersal to new geographic regions (Moore and Donoghue 2007).

All the preceding explanations are linked by a common assumption that species richness within clades is limited by the net rate of species diversification, where the net diversification rate is simply the difference between speciation and extinction rates. Should a new trait arise within a lineage that increases the rate of speciation, clade diversity is expected to increase more rapidly than it would have without the trait. However, an alternative explanation is that species richness within clades is determined by ecological limits on clade growth (Ricklefs 2006, 2007, 2009; Rabosky 2009a, 2009b). This is an idea with deep roots in the paleontological literature, where researchers have long debated whether Phanerozoic diversity patterns reflect equilibrium/saturation dynamics or whether they reflect exponentially increasing diversity toward the present (Raup 1972; Raup et al. 1973; Sepkoski 1984; Alroy et al. 2008; Benton 2009).

In this framework, a trait that results in an increase in the rate of speciation will have no effect on clade diversity except during the earliest stages of an evolutionary radiation: Once diversity has reached some form of limit, any increase in the speciation rate will be offset by a corresponding increase in the extinction rate. These paradigms lead to substantially different predictions about the relationship between species richness and time (Fig. 1). Moreover, diversification rates cannot even be meaningfully estimated from data on extant species richness and clade age if the ecological limits model applies (Rabosky 2009a). Consider two clades with identical diversification-through-time patterns, differing only in age (Fig. 1c). If we assume that diversity is rate limited, we will mistakenly infer that the younger clade has a higher rate of diversification than the older clade under simple estimators of diversification rates (Magallon and Sanderson 2001).

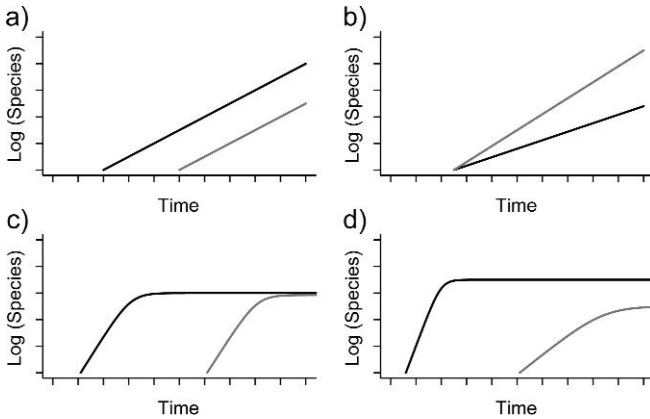


FIGURE 1. Alternative processes to explain the variation in species richness among clades, as illustrated by trajectories of species richness through time for two clades starting with a single ancestral species. a) Species richness among clades differs because clades with identical net diversification rates vary in age; older clades have more species than younger clades. b) Clades of the same age differ in species richness because of differences in the net rate of species diversification. c) Two clades that differ in age have similar species richness because they have similar ecological limits. d) Two clades differ in species richness because they have different ecological limits. Note that (a) and (b) imply that nonequilibrium processes shape the distribution of species richness among clades, whereas ecological limits (c, d) posit a role for equilibrium or diversity-dependent processes. The trajectories shown in (c) and (d) represent cases where estimation of diversification rates is positively misleading because rate estimates are confounded by clade age and bear no relationship to the true tempo of species accumulation within clades. In (c), the younger clade would be estimated to have a higher diversification rate than the older clade despite no difference in the underlying pattern of diversification through time. In (d), the older clade has a greater ecological limit than the younger clade and reaches the limit more quickly through a faster net diversification rate. However, the younger clade is inferred to have a faster rate of diversification, simply because it is young.

This dichotomy between rate-limited and ecological limits models of diversity necessarily ignores many complexities of the diversification process. However, the overwhelming majority of research in this area has implicitly assumed the validity of the rate-limited model (Fig. 1a,b) in the estimation of diversification rates from phylogenetic data. Untested, this assumption can lead to incorrect conclusions regarding controls on species richness and geographic variation in diversification rates as well as the interpretation of sister-clade contrasts (Rabosky 2009a). It is thus imperative that researchers critically examine whether empirical patterns are best explained by rate-limited or ecological limits models prior to making inference about speciation and extinction in the absence of paleontological data.

Here, I use a likelihood framework to distinguish between these general models using data consisting of clade ages and species richness for extant taxa only. I use hierarchical models to explicitly relax the assumption of rate constancy among lineages and apply the framework to a recent time-calibrated phylogeny of ants. I demonstrate that net diversification rates do not exert primary control on species richness in this group and suggest that variation in diversity among clades is bet-

ter explained by a model that posits ecological limits on clade growth.

METHODS

Estimation Under the Simple Birth–Death Process

Under the birth–death process (Kendall 1948), lineages undergo speciation at a per-lineage rate λ and go extinct at per-lineage rate μ . For phylogenetic studies of diversification, it is convenient to reparameterize the birth–death process in terms of the net diversification rate, r , and the relative extinction rate, ε (Nee et al. 1994). The net diversification rate is simply the difference between speciation and extinction ($r = \lambda - \mu$), and the relative extinction rate is the ratio of the extinction rate to the speciation rate ($\varepsilon = \mu/\lambda$). All models presented below assume that a common relative extinction rate applies to all clades in the data set.

The data D consist of N clade ages (t_1, t_2, \dots, t_N) with associated species richness data (n_1, n_2, \dots, n_N), which we can use to estimate both r and ε . Assuming rate constancy through time, the probability that a single lineage will, after some amount of time, result in a total of n_i surviving lineages is

$$\Pr(n_i|r, \varepsilon, t_i) = (1 - \beta_i)\beta_i^{n_i-1}, \quad (1)$$

where

$$\beta_i = \frac{e^{n_i} - 1}{e^{n_i} - \varepsilon}. \quad (2)$$

This model is conditioned on clade survival to the present ($n_i > 0$) and assumes that $r > 0$ and $\varepsilon < 1$.

I assume here that clades are descended from a single ancestral lineage as is typical for many molecular phylogenies where the stem clade age can more easily be identified than the crown clade age. However, it is straightforward to extend the model to an arbitrary number of ancestral lineages, although the probability in equation 1 becomes more complicated (Raup 1985; Foote et al. 1999). By multiplying these probabilities together across all N clades, we obtain the likelihood of the data as a function of r and ε (Bokma 2003):

$$L(D|r, \varepsilon) = \prod_{i=1}^N \Pr(n_i|r, \varepsilon, t_i). \quad (3)$$

As an alternative, we can also include a model where speciation and extinction rates are exactly equal through time ($\varepsilon = 1$). Here, the probability of n_i lineages is

$$\Pr(n_i|\lambda, t_i) = \frac{(\lambda t_i)^{n_i-1}}{(1 + \lambda t_i)^{n_i+1}} \quad (4)$$

for $n_i > 0$ (Bailey 1964). The likelihood of the data can be computed as in equation 3.

Total Time-Integrated Speciation

The approach described above assumes that rates have been constant within clades through time. This

assumption is explicit in nearly all studies to date that have estimated diversification rates from clade age and species richness data. However, the ecological limits model proposes that rates should decline through time as clades approach a limiting value analogous to a carrying capacity in population biology (Ricklefs 2007, 2009; Rabosky 2009a, 2009b). Diversification under an ecological limits model presumably involves diversity-dependent feedback of species richness on speciation and/or extinction rates. As a process with a substantial deterministic component, it may be inappropriate to apply a stochastic birth and death process. For example, if species richness is regulated by diversity-dependent rates, then a process that is on average balanced ($\lambda = \mu$; $\mu > 0$) may effectively have zero probability of extinction: A drop in diversity leads to a corresponding decrease in extinction or increase in speciation, such that clades are prevented from undergoing a random walk to extinction.

As an alternative to the rate-limited birth and death process described above (equations 1 and 2), I propose that we can approximate an ecological limits process that has reached equilibrium ($\lambda = \mu$; $\mu > 0$) by a pure birth process ($\mu = 0$), with the assumption that all clades have undergone the same quantity of time-integrated speciation (Ω), where

$$\Omega = \int \lambda(t) dt. \quad (5)$$

Under this formulation of the ecological limits model, the speciation rate λ should decline to zero as clade diversity approaches a limiting value because rates are assumed to be diversity dependent (Phillimore and Price 2008; Rabosky and Lovette 2008). Thus, for clades that are no longer growing, Ω will be independent of clade age, and the expected species richness for a diversification process starting with a single ancestral lineage is

$$n = e^{\Omega}. \quad (6)$$

For clades that are no longer growing through time, Ω can be estimated as the logarithm of the observed species richness. Assuming constant Ω across all clades is identical to assuming that speciation rates within all clades have decreased through time to zero and that a common temporally declining speciation function describes the dynamics of diversification in all clades.

If all lineages have undergone the same total time-integrated speciation (with $\mu = 0$), the probability of n lineages is given by

$$\Pr(n_i|\Omega) = (1 - \Psi)\Psi^{n_i-1}, \quad (7)$$

where

$$\Psi = \frac{e^{\Omega} - 1}{e^{\Omega}}. \quad (8)$$

These expressions can be used as in equation 3. Essentially, this approach discards all information on clade

age and fits a geometric distribution to species richness data. If the data are better explained by an ecological limits model, then species richness will be best explained by a simple model that ignores information on clade age and that assumes constant Ω across all clades. However, if species richness is rate limited, the probability model defined by equations 1 and 2 will fit the data better. I refer to these models as constant- Ω and constant-rate models, respectively. The Ω model is formally equivalent to assuming that i) all clades within a data set have reached time-invariant equilibrium diversities, although these equilibrium diversities may vary among clades and ii) the distribution of equilibrium values among clades can be characterized using some particular probability model (in this case, a geometric distribution). The model requires that all clades have reached $\lambda = 0$, but it is possible to relax the assumption that Ω values are constant across clades.

It may seem odd to model species richness in higher taxa assuming a simple pure birth process. However, as I will demonstrate, even this simple model performs well in comparison to the widely used birth-death process assuming constant rates of speciation and extinction through time within clades.

Hierarchical Modeling Framework

The models described above assume that rates or Ω are constant across all clades considered. However, there is considerable evidence for variation in diversification among clades, and an ideal modeling framework would allow us to take this variation into account. Rabosky (2009b) suggested that extreme among-clade variation in diversification rates might result in a breakdown of the age-diversity relationship in higher taxa. However, available frameworks for modeling diversification assume a limited number of discrete shifts in diversification rates along the branches of phylogenetic trees (Moore et al. 2004; Rabosky et al. 2007; Alfaro et al. 2009). These approaches are difficult to compare with the simple models described above because accommodating rate heterogeneity requires a large increase in the number of parameters. In the MEDUSA framework described by Alfaro et al. (2009), allowing five net diversification rates within a single phylogenetic tree requires 9 parameters (5 r values plus 4 inferred rate-shift locations).

An alternative approach is to assume that each clade has diversification rates r_i drawn from some overall distribution (Rabosky 2010). Although we cannot observe these rates directly, we can integrate over all possible rates to make inferences about the distribution from which those rates may have been drawn. This is similar to the framework used to relax assumptions about the constancy of molecular evolutionary rates along the branches of a phylogenetic tree (Thorne et al. 1998; Drummond et al. 2006). Here, I assume that the logarithms of true (unobserved) diversification rates are normally distributed. Although the use of any particular

distribution might seem arbitrary, the lognormal is a simple well-known probability distribution, defined on the appropriate interval $(0, \infty)$ and shows great flexibility in shape. The objective is thus to characterize the distribution of diversification rates in terms of the parameters of a lognormal distribution: the mean (θ) and standard deviation (SD) (σ) of log-transformed values. The probability density of a particular species richness value n_i is then

$$f(n_i|\theta, \sigma, \varepsilon, t_i) = \int_0^\infty \Pr(n_i|r_i, \varepsilon, t_i)f(r_i|\theta, \sigma)dr_i, \quad (9)$$

where $f(r_i|\theta, \sigma)$ is the lognormal density or

$$f(r|\theta, \sigma) = \frac{1}{r\sigma\sqrt{2\pi}} \exp\left[-\frac{(\log r - \theta)^2}{2\sigma^2}\right]. \quad (10)$$

The likelihood of the full data is computed as follows:

$$L(D|\theta, \sigma, \varepsilon) = \prod_{i=1}^N f(n_i|\theta, \sigma, \varepsilon, t_i). \quad (11)$$

This expression can be maximized with respect to the lognormal parameters θ and σ . This derivation thus allows each clade to have a potentially unique r value with the addition of only a single parameter over the constant-rate model described above. This model will be referred to as the relaxed-rate model. The probability densities for each clade (equation 9) are readily computed using numerical integration, and the likelihood can be maximized using standard methods for numerical optimization. Note that this hierarchical framework allows one to study the overall magnitude of rate heterogeneity among lineages, but it is not a method for identifying specific shifts in diversification on phylogenetic trees (Sanderson and Donoghue 1996; Moore et al. 2004; Rabosky et al. 2007; Alfaro et al. 2009).

As an alternative to the relaxed-rate model, I considered a relaxed- Ω model, which assumes that Ω values are drawn from a lognormal distribution. This is the same model described by equations 9–11, except that $\Pr(n_i|r_i, \varepsilon, t_i)$ is replaced by $\Pr(n_i|\Omega)$ from equation 7. Thus, in addition to simple constant-rate and constant- Ω models, we can now consider relaxed-rate and relaxed- Ω models that explicitly relax assumptions about the homogeneity of the diversification process across lineages.

The approach described above treats clades as independent data points, but it is possible to incorporate phylogenetic autocorrelation of diversification parameters into the model. For example, one could model all rates as a draw from a multivariate lognormal distribution with a variance–covariance structure specified by the phylogeny. However, computing the probability density of n_i species requires that we integrate over all possible rates in the full set of N clades. This requires Markov Chain Monte Carlo methods or other techniques for Monte Carlo integration and will not be considered in this paper.

Data

I applied the modeling framework described above to a recent time-calibrated phylogeny of ant genera (Moreau et al. 2009; Pie and Tscha 2009). The phylogeny consists of 139 terminal taxa and includes 19/20 ant subfamilies. Pie and Tscha (2009) added species richness data to terminal clades in the Moreau et al. (2009) tree, using the ANTBASE database (Agosti and Johnson 2005). By assuming ant genera to be monophyletic, Pie and Tscha (2009) were able to assign 90% of all ant species to the tree. Thus, although the tree does not contain all ant genera, it presumably captures the prevailing mode and tempo of ant diversification (Pie and Tscha 2009). It is likely that many ant species remain to be discovered (Rabeling et al. 2008). The analyses here assume that the species richness of a given genus is proportional to its true species richness regardless of the number of cryptic or otherwise unknown species.

I evaluated the fit of six models to the ant data using maximum likelihood: 1) a constant-rate model with $\varepsilon = 0$ (e.g., a pure birth process), 2) a constant-rate model with $\varepsilon \geq 0$, 3) a constant-rate model with equal speciation and extinction rates ($\varepsilon = 1$), 4) a relaxed-rate model with $\varepsilon \geq 0$, 5) a constant- Ω model, and 6) a relaxed- Ω model. Because many studies have estimated relative extinction rates from such data, I included constant-rate models with and without extinction to assess how inferences about relative extinction rates might change depending on whether researchers assume a rate-limited model or ecological limits model of diversification. All models were fitted in the R statistical environment. Numerical optimization used the Nelder–Mead algorithm with multiple sets of random starting parameters. A log or logit transformation was applied to all parameters such that optimization occurred on the range $(-\infty, \infty)$. Models were compared using the Akaike Information Criterion (AIC).

Evaluation of Model Adequacy

Merely demonstrating the higher likelihood or posterior probability of the data under a particular model relative to some other model provides little information about model adequacy. One poor model may fit the data better than another poor model, but this does not necessarily imply that either model provides meaningful information about underlying evolutionary processes. For this reason, Bayesian statistical modeling frequently employs posterior predictive checks that ask whether fitted models make predictions that are consistent with the observed data (Gelman et al. 2003).

I evaluated model adequacy by simulating clade diversity under the maximum likelihood parameter estimates for each model. I then computed three summary statistics for each simulated data set: i) the SD of species richness across clades, ii) the maximum species richness, and iii) the Spearman correlation between clade age and species richness. If a model yields parameter estimates that are informative, it follows that those

parameter estimates should be capable of reconstructing the major features of the observed data. In this case, the variation in species richness among clades as well as the relationship between clade age and species richness are of considerable interest, as they address the magnitude of rate heterogeneity among lineages and the extent to which rates may slow through time within clades (Rabosky 2009a). The maximum species richness may provide additional information about model inadequacy. If rates slow through time, rate-limited models might predict clades with more species than observed, because this class of models typically assumes no limits on clade growth. I compared the distribution of estimates for each summary statistic under each model with the values observed for the ant data set.

Simulating species richness data are straightforward under all models considered here. The distribution of species richness for a given diversification process is geometric (equations 1 and 7) with parameter $(1 - \beta)$ or $(1 - \Psi)$, depending on whether one is modeling species richness as a function of diversification rate or Ω . Simulation of a single species richness value is performed by drawing from this distribution until the first nonzero value is obtained, as we have already conditioned on clade survival to the present. For the relaxed-rate and relaxed- Ω models, this first entails drawing a rate or Ω parameter for each clade from the fitted lognormal distribution, then drawing species richness from the corresponding geometric distribution. A total of 5000 data sets were simulated under each model.

RESULTS

Analysis of Ant Diversification

Species richness in ants is better explained by total time-integrated diversification (Ω) than by net diversification rates (Table 1). Although the relaxed-rate model provided a substantial improvement over the constant-rate model ($\Delta\text{AIC} = 78$), a relaxed- Ω model was the overall best-fit model. Likewise, a constant- Ω model fit the data much better than the corresponding constant-rate model ($\Delta\text{AIC} = 33.2$). The constant-rate model with $\varepsilon = 1$ fit the data much more poorly than all other mod-

els, suggesting that a constant-rate process with $\lambda = \mu$ is unlikely to explain the data; this model is dropped from further consideration.

Parametric simulations to assess model adequacy clearly indicate that constant-rate and relaxed-rate models cannot account for observed species richness in ants (Fig. 2). For all three metrics, a constant-rate model with $\varepsilon = 0$ performs poorly, predicting much higher variation in species richness and maximum clade richness relative to the observed data as well a strong positive relationship between clade age and species richness. Both constant-rate and constant- Ω models predict lower variance in species richness among-clades relative to the observed data. However, the constant-rate model also predicts a positive correlation between clade age and species richness, which is not observed in the ant data. Although the likelihood of the data is much higher under the relaxed-rate model relative to the constant-rate model, the relaxed-rate model cannot recover any of the major features of the ant data. Specifically, the relaxed-rate model predicts too much variation in clade size, excessively large maximum clade sizes, and a positive correlation between age and species richness. Only the relaxed- Ω model can reconstruct the variation in species richness, the maximum clade size, and the correlation between age and diversity observed for the ant data.

I compared the order statistics of expected species richness under both relaxed-rate and relaxed- Ω models (Fig. 3). These analyses show that expected clade sizes under the relaxed-rate model are much larger than the rank-ordered counterpart from the real data set. Although the relaxed-rate model predicts a maximum species richness that far exceeds the observed value for the ant data set (Fig. 2), it is true more generally that the k 'th largest clade under this model is predicted to contain more species than the k th largest ant clade. This is not true for the relaxed- Ω model, where there is considerable overlap between observed and expected species richness. Although true ant species richness is almost certainly underestimated, it is important to remember that the models were parameterized from this incomplete data set. Thus, the excessive species diversity predicted under the relaxed-rate model cannot be explained by potential discrepancies between true (unknown) ant diversity and the values analyzed in this and other studies (Pie and Tscha 2009).

TABLE 1. Summary of diversification models fitted to the ant data set

Model	LogL	AIC	np ^a	Parameters ^b
Constant rate ($\varepsilon = 0$)	-951.6	1905.2	1	$r = 0.0746$
Constant rate ($\varepsilon \geq 0$)	-758.9	1521.8	2	$r = 1.34 \times 10^{-7}$; $\varepsilon = 0.999999$
Constant rate ($\varepsilon = 1$)	-1326.6	2655.2	1	$\lambda = \mu = 0.662$
Constant- Ω	-743.3	1488.6	1	$\Omega = 4.35$
Relaxed rate	-718.9	1443.8	3	$\theta = -6.27$; $\sigma = 1.05$; $\varepsilon = 0.999$
Relaxed- Ω	-712.6	1429.2	2	$\theta = 1.19$; $\sigma = 0.28$

Notes: ^aNumber of parameters in each model.

^b λ = speciation rate; μ = extinction rate; r = net diversification rate, $\lambda - \mu$; ε = relative extinction rate, μ/λ ; Ω = total time-integrated speciation; θ = mean of lognormal distribution; σ = SD of lognormal.

Extinction Estimates

One of the most striking results from this analysis is the massive improvement in model fit under a constant-rate birth-death model ($\varepsilon \geq 0$) relative to a constant-rate pure birth ($\varepsilon = 0$) model ($\Delta\text{AIC} = 383.4$). Under both constant-rate and relaxed-rate models, ε is estimated as exceeding 0.999 consistent with high species turnover through time. I computed profile likelihood confidence intervals on this parameter for rate-limited models (Table 2). Under the constant-rate and relaxed-rate models, we are confident that this parameter exceeds 0.99

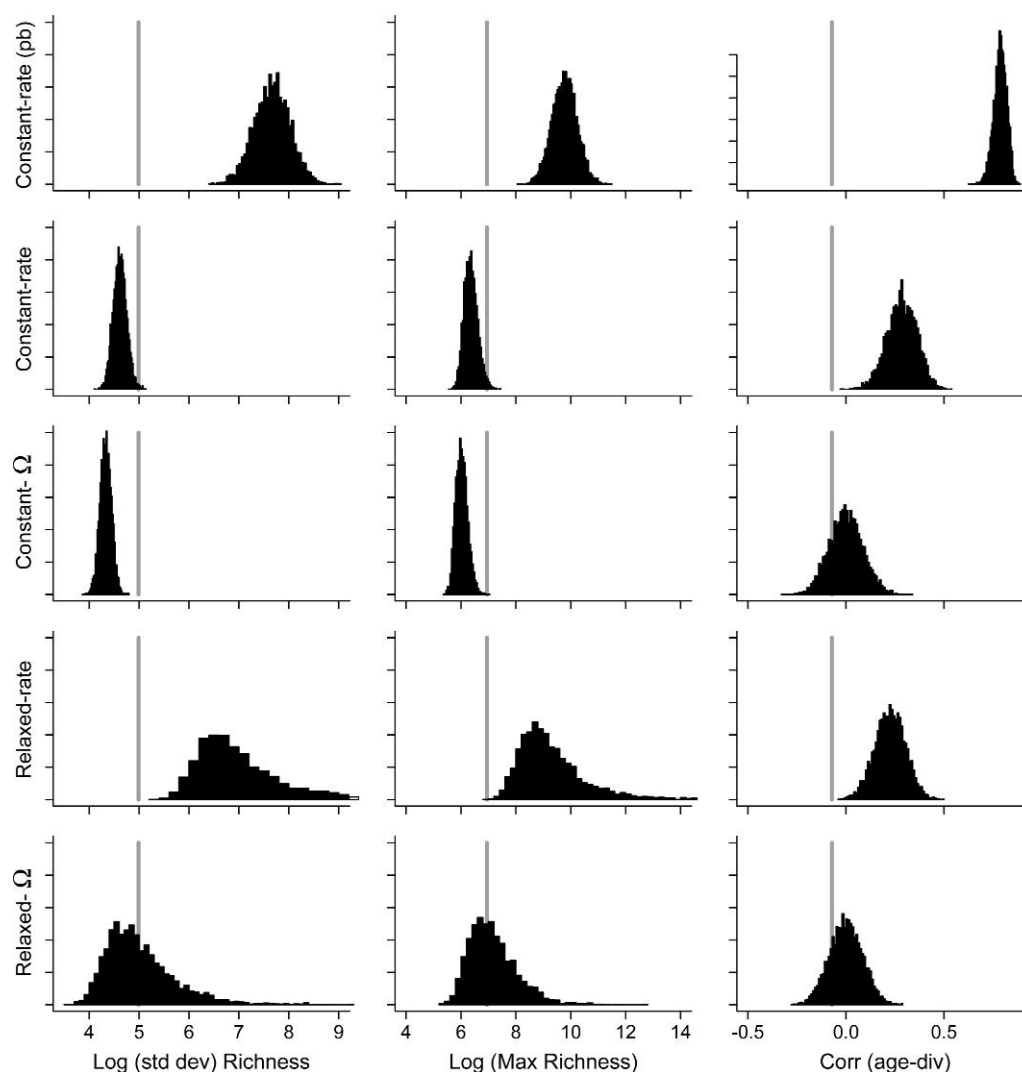


FIGURE 2. A posteriori evaluation of model adequacy for five fitted diversification models (rows). Shown are distributions of a) the SD of species richness among clades within simulated data sets; b) the maximum species richness noted for each simulation; and c) the correlation between clade age and species richness. Observed values for the ant data set are denoted by gray lines. Both the SD and maximum species richness have been log transformed for clarity of presentation. The three rate-limited models failed to recover any of these features of the observed data. The constant- Ω model recovered the observed correlation between clade age and species richness; simulations conducted under the relaxed- Ω model gave results consistent with the observed data for all three summary statistics. Simulations were parameterized using maximum likelihood estimates (Table 1), and 5000 simulated data sets were generated under each model.

(Table 2). Because a number of studies have estimated extinction rates from similar data, I will consider the problems with these estimates in detail.

Estimates of high ϵ under constant-rate and relaxed-rate models appear to result from violation of the underlying assumption that rates within clades have been constant through time. Three lines of evidence support this contention. First, the ecological limits models, which assume $\mu = 0$, fit the data much better than the rate-limited models considered (Table 1 and Fig. 2). Second, confidence in our estimates of ϵ far exceeds what is possible, even if the data were generated under a constant-rate model with high ϵ . To demonstrate this, I simulated 5000 data sets under a constant-rate model using maximum likelihood parameter estimates

for the ant data for this model (Table 1: $r = 1.34 \times 10^{-7}$; $\epsilon = 0.9999$). For each simulated data set, I fitted both a constant-rate model with $\epsilon \geq 0$ and a constant-rate model with $\epsilon = 0$. I then tabulated the difference in AIC scores between these models (Fig. 4). Essentially, this asks the following: if the constant-rate model with high ϵ is the true model, how much better would this model fit the data relative to a simple constant-rate model with no extinction ($\epsilon = 0$)? This is a straightforward but important comparison because the observed results suggest an enormous degree of confidence in high extinction relative to a constant-rate model with $\epsilon = 0$ (Table 1). Results indicate that the observed level of support for a rate-limited model with high ϵ relative to a rate-limited model with $\epsilon = 0$ ($\Delta\text{AIC} = 383.4$) is

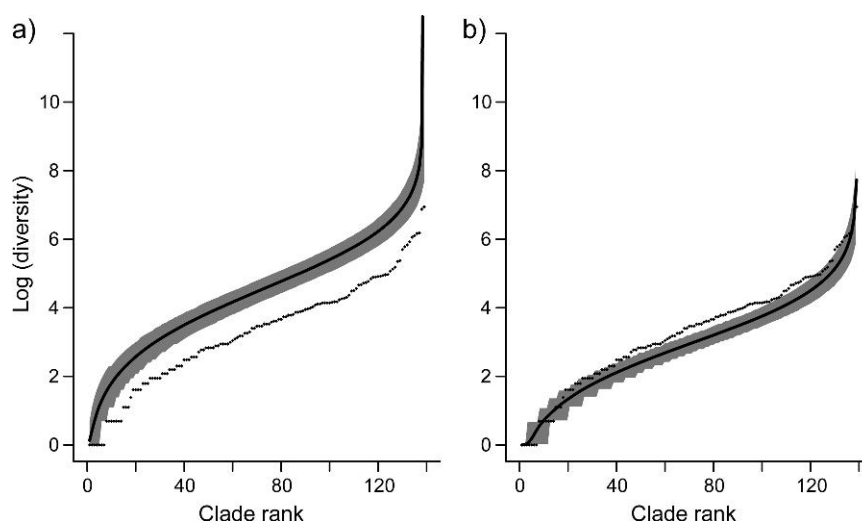


FIGURE 3. Rank ordering of expected species richness for data sets simulated under a) relaxed-rate and b) relaxed- Ω models. Dots indicate observed species richness for the ant data set. Line represents mean species richness from simulations, and shaded regions denote 2.5% and 97.5% quantiles of the simulated values. The relaxed-rate model predicts excessively species-rich clades, but the relaxed- Ω model shows considerable overlap with the observed data. Note that species richness is log-transformed.

improbably high, even if the true evolutionary model was constant rate with high ε ($p \sim 0$).

A third line of evidence is that, when species richness data are simulated under a constant- Ω model but analyzed under a constant-rate model, extinction estimates are severely biased. To demonstrate this, I simulated 5000 data sets under the best-fit parameterization of the constant- Ω model ($\Omega = 4.35$; Table 1). I then estimated ε for each simulated data set using the constant-rate birth–death model (equation 3). All estimates under the constant-rate model converged on the limiting value of $\varepsilon = 1.0$, and our inferred confidence in those estimates is high (Fig. 5). Identical results are obtained when data are analyzed under a relaxed-rate model. Taken together, these results indicate that, when the data are best explained by constant- Ω or relaxed- Ω models, extinction rate estimates are fraught with problems.

DISCUSSION

The estimation of diversification rates from clade age and (extant) species richness data requires that net diversification rates control clade diversity through time (Fig. 1). When clade diversity is no longer increasing through time, this assumption is violated, with severe consequences for the estimation of diversification rates. Specifically, the estimated rates will scale negatively

with age: Old clades may have undergone the same amount of total time-integrated speciation (Ω) as young clades and with precisely the same diversification rates through time, but lower rates will be inferred for old clades because we will have inappropriately corrected for clade age (Rabosky 2009a).

Hundreds of studies have attempted to infer net diversification rates by assuming that diversity is limited by net diversification rates, using estimators from the time-homogeneous birth–death process (after Bailey 1964; Raup 1985; Foote et al. 1999; Magallon and Sanderson 2001). However, researchers rarely test whether their

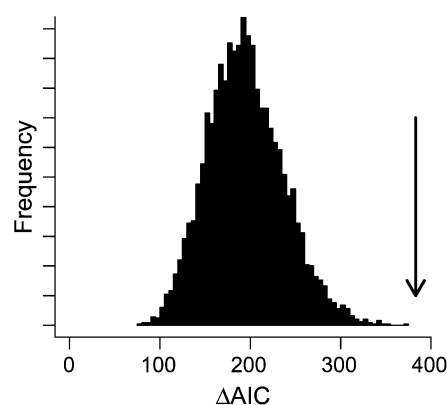


FIGURE 4. Expected distribution of the difference in AIC scores (ΔAIC) between constant-rate pure birth ($\varepsilon = 0$) and constant-rate birth–death ($\varepsilon \geq 0$) models when data are simulated under a constant rate birth–death model using parameters inferred for the ant data set (Table 1: $r = 1.34 \times 10^{-7}$; $\varepsilon = 0.999999$). Arrow indicates ΔAIC value observed for the ant data. These results indicate that observed support for high relative extinction rates is much too high: This level of support could not be observed, even in principle, if a constant-rate birth–death model was the true model.

TABLE 2. Relative extinction rates and 95% confidence intervals estimated using the profile likelihood method

Model	ε	95% CI
Constant rate ($\varepsilon \geq 0$)	0.9999999	(0.999, 1)
Relaxed rate	0.999	(0.993, 1)

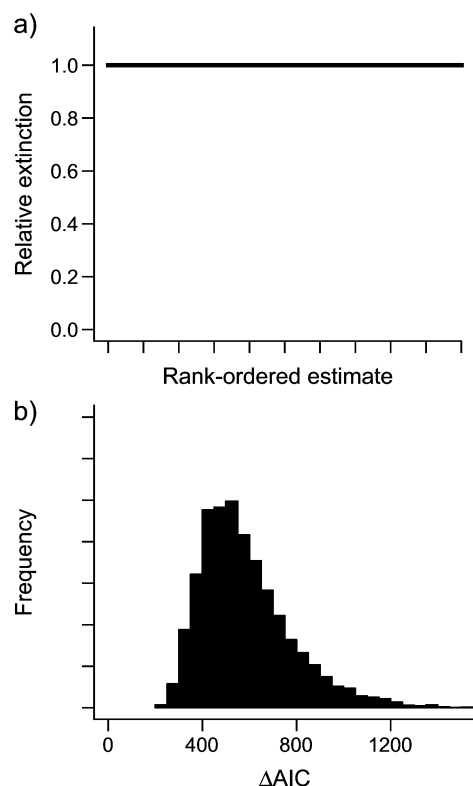


FIGURE 5. When data are simulated under an ecological limits model (constant- Ω), relative extinction estimates under rate-limited models are nonsensical. a) Rank-ordered estimates of relative extinction rates from 5000 data sets simulated under constant- Ω model with $\Omega = 4.35$. All estimates converged on the limiting value of $\varepsilon = 1$, even though there is no term corresponding to relative extinction in the Ω models. b) Distribution of the difference in AIC scores (ΔAIC) between constant-rate pure birth ($\varepsilon = 0$) and constant-rate birth-death ($\varepsilon \geq 0$) models for constant- Ω data sets described above. The extreme bias in relative extinction estimates is accompanied by high confidence in those estimates.

data violate the most fundamental assumption of rate-limited models. Simply stated, these approaches assume that clades grow continuously through time and that diversity is not limited by ecological or other factors. Violation of this assumption has consequences that go far beyond simple bias in the estimation of diversification rate and leads to positively misleading inferences about the causes of variation in diversity at numerous levels (Rabosky 2009b).

Here, I presented a framework for testing whether rate-limited models provide an adequate description of patterns of standing species richness within clades. The approach I advocate entails comparing the fit of models that assume primary control of diversity by variation in net diversification rates (rate-limited models) relative to models that assume diversity is regulated by ecological factors. I applied this framework to a recent higher-level phylogeny of ants and found that a simple ecological limits model provided a much better fit to the data than rate-limited models. These results hold even when the assumptions of constant diversification among clades

are relaxed. The notion that clade diversity may be regulated by ecological factors is consistent with numerous observations from the fossil record across larger phylogenetic and temporal scales, including apparent equilibrium dynamics of species richness across the Phanerozoic (Raup 1972; Rosenzweig 1975; Alroy et al. 2008), diversity dependence of origination and extinction rates (Foote 2000; Alroy 2008), and rapid diversity rebounds after mass extinction events (Stanley 1979; Brayard et al. 2009).

Ecological Limits and Ω

Here, I have defined Ω as total time-integrated speciation experienced by a clade. Under a model where clade diversity is regulated by ecological limits (Ricklefs 2007, 2009; Ricklefs et al. 2007), this quantity should cease to increase through time once clades have reached a limiting diversity. The Ω model as described here is clearly an incomplete description of reality: It assumes that extinction does not occur, yet the fossil record indicates that extinction rates are often high relative to speciation rates (Stanley 1979; Gilinsky et al. 1994; Alroy 2008). I suggest that omitting extinction from the model is not as problematic as it might seem. If clade diversity is governed by equilibrational mechanisms, such that rates of speciation and/or extinction are diversity dependent, then the probability of clade extinction may be much lower, on a given time-interval, than would be expected under a simple birth-death process. Under a balanced ($\lambda = \mu$; $\mu > 0$) birth-death process, we expect a positive relationship between clade age and species richness to arise simply because small clades are more likely than large clades to undergo a random walk to extinction (e.g., Rabosky 2009b; Fig. 1b). Such a balanced process should leave us with the perception that clade diversity has continued to increase through time due to positive net diversification rates solely because small clades are more likely than large clades to drift to the absorbing boundary (e.g., extinction; $N = 0$) on a given time interval. As there is no positive relationship between clade age and species richness, it is unlikely that a balanced and unregulated diversification process could give rise to observed patterns of ant species richness. This is further reflected by the poor fit of the balanced model (equation 3) relative to all other models under consideration.

It is unclear why a geometric (constant- Ω) or modified geometric (relaxed- Ω) model would provide a reasonable fit to the observed distribution of species richness. That a hierarchical geometric model with log-normally distributed Ω values provides the best overall fit to the data would suggest that there is more variation in clade size than can be explained by a simple geometric distribution (Fig. 2). The Ω model can alternatively be interpreted as describing a process of diversification where species richness is governed by a strictly deterministic model where the net diversification rate is zero. In this case, species richness from a single

ancestral lineage is a function of total time-integrated net diversification or

$$N = e^{\int [\lambda(t) - \mu(t)] dt}, \quad (12)$$

but where the value of the integral is a random variable describing the distribution of equilibrium values or carrying capacities occupied by a set of clades. If standing diversity within clades is a function of clade-specific ecological limits, then perhaps our focus should shift toward understanding the factors that govern the distribution of “ecological opportunities” available for radiating clades.

In some groups, there is support for the idea that ecological limits might be related to geographic area and latitude (Ricklefs 2006). These analyses constitute much stronger evidence for the ecological limits model because they directly link ecological attributes of clades to patterns of species richness. In the absence of additional ecological data, the ecological limits model is simply an a priori expectation for patterns of species richness within higher taxa based on the assumption that species within clades to which we assign names (families, orders, tribes, etc.) might be characterized by equilibrial dynamics (Foote 2000; Alroy 2008, 2009).

However, rejection of a rate-limited model does not constitute strong evidence in favor of ecological limits on clade growth. For the ant data set, it is clear that rate-limited models, with or without heterogeneous diversification among clades, fail to describe the major patterns of species richness with respect to clade age. Although these results are consistent with the idea that ecological factors limit species richness within clades, a number of alternative explanations might also explain the observed patterns. I consider several possibilities below.

There have been few investigations of the manner by which higher taxa are designated as such by systematists, and we do not know at present how such sampling biases influence the apparent relationship between age and diversity. It is clear that higher taxa are a nonrandom subset of clades from the tree of life, but we know little about the nature of this nonrandomness and its implications for the study of diversification. If higher taxa are named precisely because they correspond to clades within which equilibrial dynamics occur, this raises interesting questions about the factors that determine those dynamics.

If higher taxa are recognized, implicitly or explicitly, by ecological and phenotypic attributes that define a particular “adaptive zone” (Simpson 1953), then it is possible that these clades would effectively delineate a fixed pool of resources that might in turn limit the number of species within clades. In fact, if the ecological limits model proves to play a significant role in explaining species richness in higher taxa, this would represent a validation of Simpson’s basic ideas concerning the origin of higher taxa and subsequent diversification within novel adaptive zones. In this framework, the differences between clades we recognize as higher taxa reflect discontinuities between adaptive zones. Simpson

(1953) devoted an entire chapter of “The major features of evolution” to the problem of higher taxa and their relationship to adaptive zones.

Alternatively, clades might correspond to biogeographically cohesive groups. Although systematists might not use geography directly in the delimitation of higher taxa, it is certainly plausible that they are more likely to recognize clades that are monophyletic within major geographic regions. In turn, this would imply that clades define distinct geographic theatres for diversification, such that diversity within clades would be limited by evolutionary species–area relationships (Rosenzweig 1995; Losos and Schluter 2000), environmental energy, or other factors.

The issue of sampling can be framed in terms of a paradox: If we had a complete phylogenetic tree for all species of ants (or other taxon), there would almost certainly be a positive relationship between age and diversity for clades drawn at random from that tree. The hierarchical structure of a tree requires that younger clades be nested within older more inclusive clades. On average, older clades should thus be more diverse than younger clades. Yet, we do not observe this relationship in the set of clades corresponding to recognized higher taxa. What is it about this set of taxa that leads to a breakdown of the age–diversity relationship? The most worrisome possibility is that the selection process by which systematists delimit higher taxa results in no relationship between age and diversity regardless of the underlying factors influencing diversity dynamics. The likelihood of this latter possibility is difficult to evaluate at present.

An alternative explanation is that higher taxa have what might be termed a “life expectancy.” For example, marine invertebrate genera show a pattern of symmetric waxing and waning in the fossil record (Foote 2007; Foote et al. 2007). Species richness within taxa is low at both the beginning and the end of the taxon’s history. Under the birth–death model, the expected relationship between clade age and species richness is hump shaped if we condition on clade extinction at some point in time (Foote 2007). Although there is strong support for this model as applied to morphologically cohesive higher taxa in the fossil record (Gould et al. 1977), it is not clear whether it should apply to phylogenetically defined clades in the present context. There is no evidence that the relationship between species richness and age is hump shaped (Ricklefs 2006; McPeck and Brown 2007; Linder 2008; Rabosky 2009b), although this has not been rigorously tested. More importantly, this basic model appears logically inconsistent if we restrict our analysis to monophyletic groups: If clades have a characteristic rise and fall, then ultimately all clades will become extinct and there will be no diversity. Whatever the cause of the pattern, this appears to be more relevant to higher taxa in the fossil record, which may not be monophyletic (but see Jablonski and Finarelli 2009).

Other factors may shape the relationship between age and diversity in extant taxa, including the effects of mass extinction and associated diversity rebounds

(Erwin 1998; Sepkoski 1998). However, it is difficult to imagine how any simple time-dependent stochastic process, including mass extinction events, can entirely eliminate the expected positive age–diversity relationship for monophyletic groups.

Estimation of Diversification Rates

Regardless of the interpretation of Ω , two general conclusions can be made concerning the estimation of diversification rates. First, if a rate-limited model fails to explain patterns of species richness in a particular group, then diversification rates cannot be estimated. If species richness is not the result of a time-dependent process, then there is no meaningful rate that can be extracted from the data in the absence of diversity information from the fossil record. Rates presented in many previous studies have likely been confounded by variation in clade age and bear no necessary relationship to the actual underlying evolutionary rates (Rabosky 2009a). Even if the relationship between clade age and diversity can be attributed to biases associated with clade delimitation or to a characteristic rise and fall of diversity through time (Foote 2007)—rather than ecological limits—then many or most attempts to extract speciation and extinction rates from clade age and species richness data will not have been valid.

Second, inferences about extinction that assume rate-limited models can be severely compromised if ecological limit-based models provide a better explanation for the data. I have shown that the estimates are biased to such an extent that they may be described as nonsense; equally worrisome is the misleading confidence obtained in those estimates (Table 2 and Figs. 4–5). However, the results of this study should not be construed to imply that extinction rates have been low. Overwhelming evidence from the fossil record suggests otherwise (Alroy 1996; Bokma 2008; Quental and Marshall 2009, 2010). Here, extinction estimates perform poorly because of the inadequacy of the constant-rate birth–death model. The lack of relationship between clade age and species richness forces the rate-dependent models to attempt to equalize speciation and extinction rates because a true zero-net-diversification process should have a much weaker relationship between clade age and species richness than a process with $r > 0$. However, it is nonetheless unlikely that we would be observing 139 ant clades with substantial species richness if r had truly been zero across the history of the radiation; this is reflected in the poor fit of the constant-rate model with $\varepsilon = 1$. Thus, we consistently estimate extremely high relative extinction rates and low (but nonzero) net diversification rates under rate-limited models, when ecological limits-type models provide a better explanation for the data.

This is a serious concern for all studies that have estimated extinction rates from clade age and species richness data. As such, this joins a growing number of studies that have pointed out problems associated

with the estimation of extinction from data on living species only (Crisp and Cook 2009; Rabosky 2009c, 2010; Quental and Marshall 2010).

Summary

The notion that net diversification rates can be estimated from clade age and species richness data is a hypothesis to be tested and cannot be assumed a priori. This is a statistical question with broad biological implications. If species richness within clades is not a function of net diversification rates, alternative explanations must be considered. Constraints on diversification imposed by ecological limits can potentially explain patterns of species richness in ants and other taxa. At the very least, the data are far more consistent with this possibility than with the hypothesis that net diversification rates exert primary control on species richness. These results raise fundamental questions about the role of equilibrium and nonequilibrium processes in shaping patterns of biological diversity at the largest scales. However, a more direct approach is needed to infer the nature of ecological limits. Many studies have assessed potential ecological covariates associated with high species richness. However, few have explicitly tested whether these covariates are likely to influence net diversification rates or ecological limits, and the interpretation of much of this work is unclear.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.sysbio.oxfordjournals.org/>.

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