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RATES OF MORPHOLOGICAL EVOLUTION ARE CORRELATED WITH SPECIES RICHNESS IN SALAMANDERS

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The tempo and mode of species diversification and phenotypic evolution vary widely across the tree of life, yet the relationship between these processes is poorly known. Previous tests of the relationship between rates of phenotypic evolution and rates of species diversification have assumed that species richness increases continuously through time. If this assumption is violated, simple phylogenetic estimates of net diversification rate may bear no relationship to processes that influence the distribution of species richness among clades. Here, we demonstrate that the variation in species richness among plethodontid salamander clades is unlikely to have resulted from simple time-dependent processes, leading to fundamentally different conclusions about the relationship between rates of phenotypic evolution and species diversification. Morphological evolutionary rates of both size and shape evolution are correlated with clade species richness, but are uncorrelated with simple estimators of net diversification that assume constancy of rates through time. This coupling between species diversification and phenotypic evolution is consistent with the hypothesis that clades with high rates of morphological trait evolution may diversify more than clades with low rates. Our results indicate that assumptions about underlying processes of diversity regulation have important consequences for interpreting macroevolutionary patterns.

KEY WORDS: **Adaptive radiation, macroevolution, morphological evolution, phylogenetics, speciation.**

Explaining the variation in both species richness and phenotypic diversity across the tree of life is a major challenge in evolutionary biology. Previous studies have demonstrated that rates of both species diversification and phenotypic evolution vary widely among clades (e.g., Alfaro et al. 2009; Eastman et al. 2011; Venditti et al. 2011), but we are only beginning to directly investigate the potential relationships between these patterns and the processes that generate them (Adams et al. 2009). There are many reasons to expect positive correlations between rates of phenotypic evolution and rates of species diversification. For example, high rates of phenotypic evolution might lead to high speciation rates because the capacity for rapid local adaptation might lead to rapid evolution of prezygotic isolation mechanisms between populations. Indeed, the theory of "punctuated equilibrium" was proposed in part to explain the observation that phenotypic change in the fossil record frequently appears to be associated with speciation (Eldredge and Gould 1972).

The capacity for rapid phenotypic evolution may directly facilitate species diversification by increasing the ability of a radiating clade to exploit ecological opportunity (Parent and Crespi 2009; Slater et al. 2010; Martin and Wainwright 2011). Clades with high rates of phenotypic evolution should have increased

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ability to explore ecological space and should diversify more than clades with low phenotypic rates if there are strong ecological controls on species richness. The idea that such "evolvability" might promote species diversification via ecological mechanisms has a long history in evolutionary biology and is fundamental to understanding the ecological mechanisms underlying key evolutionary innovations (Liem and Osse 1975; Heard and Hauser 1995). Vermeij (1973a,b) proposed that groups with high evolutionary lability in form ("versatility" sensu Vermeij 1973a) have replaced less-labile groups through time, perhaps due to the ability of high-lability groups to better utilize a broader spectrum of available resources (e.g., by increasing the overall size of the realized adaptive zone: [Vermeij 1973a]).

Although correlations between rates of phenotypic evolution and rates of species diversification may be expected a priori, few studies have directly investigated this question. Several studies have demonstrated that rates of phenotypic evolution may be elevated during periods of time when rates of species diversification are highest (Harmon et al. 2003; Mahler et al. 2010), but these results do not necessarily imply that lineages with high rates of phenotypic evolution diversify more than lineages with low rates of phenotypic evolution. Ricklefs (2004) suggested that morphological disparity and species diversity were correlated across major clades of passerine birds, but subsequent analyses indicated that such correlations can potentially be attributable to variation in the ages of clades alone (e.g., with no variation in either rates of species diversification or phenotypic evolution; Purvis 2004; Ricklefs 2006).

Recently, Adams et al. (2009) used a phylogenetically explicit approach to estimate rates of phenotypic evolution in clades of plethodontid salamanders. They tested whether these phenotypic rates were correlated with clade-specific estimates of net diversification rates, which were computed from the estimated crown clade ages and extant species richness (Magallon and Sanderson 2001). Despite considerable among-clade variation in rates of both species diversification and phenotypic evolution, they found no evidence for a general relationship between phenotypic evolutionary rates and rates of species diversification. Rates of body size and shape evolution were uncorrelated with net rates of species diversification across the 15 clades they considered.

The analysis in Adams et al. (2009) assumed that net rates of species diversification could be inferred for each salamander clade from the ages of those clades in conjunction with their standing species richness. The estimators used in this and many other studies make the simple assumption that clades begin radiating from one or two ancestral lineages (for stem and crown clades, respectively), and that speciation and extinction rates have been constant in time throughout the entire history of the clade. These estimators are termed constant-rate (CR) estimators. Thus, for a clade of N extant species beginning with a single ancestral lineage some t years before the present and in the absence of extinction, the net diversification rate is simply $\log(N)/t$. Almost all published analyses of diversification in higher taxa have used variations on this basic equation, with the specific choice of CR estimators differing only in assumptions about extinction rates, the number of ancestral lineages, and whether the estimates of net diversification rates are conditioned on clade survival to the present (Magallon and Sanderson 2001; Wiens 2007; Alfaro et al. 2009). The theory underlying the CR estimators (Bailey 1964; Raup 1985) can easily be extended to scenarios where rates vary through time (Rabosky 2009b,2010b), although this is rarely done.

By applying CR estimators to species richness within clades, researchers explicitly assume that diversity is a function of the net rate of species accumulation through time. An alternative approach is not to assume rate constancy, but rather to model species diversification under some nonconstant process of diversification through time. One candidate process involves diversity dependence of speciation and/or extinction rates, an idea with a rich history in the paleontological literature (Rosenzweig 1975; Sepkoski 1978; Walker and Valentine 1984; Alroy 2008). In one of the earliest paleobiological applications of computer simulation, Raup et al. (1973) compared patterns of clade diversification in the fossil record to those generated under a null model that explicitly included diversity equilibria. Their use of an equilibrium diversity model was motivated in part by a general sense that diversity dependence provided a far better description of empirical patterns than a model of unconstrained diversity increase through time. More recently, a number of neontological studies have suggested that temporal patterns of speciation in molecular phylogenies are consistent with diversity-dependent regulation of speciation–extinction dynamics (Weir 2006; McPeek 2008; Rabosky and Glor 2010; Etienne et al. 2011).

Several studies have demonstrated that distributions of species richness across clades are inconsistent with a CR diversification process and suggestive of diversity-dependent control (Ricklefs 2007; Rabosky 2010b; Vamosi and Vamosi 2010) or extinction-driven clade dynamics (Pyron and Burbrink 2011). Because diversity dependence can lead to a breakdown of the relationship between clade age and species richness, CR estimators may simply covary with clade age in a manner that is largely decoupled from the factors that determine clade diversity (Rabosky 2009a). To better understand the factors that influence species richness within clades, it is important to test whether CR estimators provide a reasonable estimate of clade diversification histories before using CR-based estimates in subsequent analyses.

Here, we examine the relationship between clade diversification and phenotypic evolutionary rates in plethodontid salamanders. The premise of our article is that the validity of CR estimators cannot be assumed a priori, but must be tested by researchers before examining the relationship between species

diversification and other factors. If species richness within clades cannot be modeled adequately as a time-dependent process, then it is not appropriate to analyze and/or compare CR diversification estimates for clades. A major goal of diversification studies is to understand the factors that influence species richness within clades, and the relevant question is thus whether we should "correct for time" by computing net diversification rate estimates for clades or whether we should directly investigate correlations between clade richness and phenotypic/ecological covariates.

In addition, we also investigate a recent test proposed to assess the validity of CR estimators (Wiens 2011) and find that it is characterized by unacceptable error rates. We then apply a hierarchical Bayesian model for describing patterns of diversification rate variation among clades, and we use posterior predictive simulation to test whether this model can explain the relationship between age and diversity in the salamander dataset. We modeled the dynamics of speciation through time within salamander clades to test whether temporal declines in diversification rates could explain the observed decoupling between age and species richness. We explicitly compare the predictive ability of CR rate estimates and log-transformed richness in explaining the variation in phenotypic evolutionary rates among salamander clades. Our results suggest that CR estimators applied to plethodontid salamanders are not valid and that log-transformed species richness is a more appropriate summary of clade diversification. We find strong support for coupling between species richness and rates of phenotypic evolution.

Materials and Methods

DATA AND ESTIMATION OF PHENOTYPIC RATES

Phylogenetic data and morphological rate estimates were taken from Adams et al. (2009). The data include a time-calibrated molecular phylogenetic tree for 191 species of plethodontid salamanders comprising 15 focal clades, and estimates of species richness and crown ages for each clade. The plethodontid phylogeny was estimated from maximum likelihood analysis of nuclear and mitochondrial DNA and made ultrametric using penalized likelihood; full details are available in Adams et al. (2009) and Kozak et al. (2009).

Rates of both body size and shape evolution were obtained from morphometric analysis of 190 species distributed across the focal clades (Adams et al. 2009). Briefly, seven standard morphometric variables were measured for each of 1573 adult salamander individuals (a mean of 6.7 individuals per species). A principal components analysis (PCA) was performed on the covariance matrix of log-transformed measurements for individuals, and mean PC scores were computed for each species. Because all variables had comparable and positive loadings on PC1, this variable was treated as an overall index of body size. PC2–PC7 were treated as indices of body shape. Species' mean scores for each principal component were used to estimate rates of phenotypic evolution under a Brownian motion process. The estimated evolutionary rate for PC1 was taken as an index of the rate of size evolution. A matrix of shape rates, along with their estimated covariances, was estimated from PC2–PC7 scores. The sum of the diagonal elements of this matrix was taken as an overall estimate of the rate of body shape evolution (McPeek et al. 2008). These estimates of evolutionary rates are independent of the number of species sampled from each clade as well as the amount of time available for diversification in each clade, unless rates themselves are correlated with clade richness and/or if a model of time-invariant Brownian motion fails to describe the data.

Three lines of evidence suggest that our phenotypic evolutionary rates are valid. First, a simple Brownian motion process provides a reasonable fit to both size and shape rates of phenotypic evolution and outperforms an Ornstein–Uhlenbeck (OU) model for 13 of 15 clades (Adams et al. 2009). Second, if phenotypic rates are confounded with clade age, perhaps due to constraints or the scaling of rates with timescale of measurement (Gingerich 2001), then we should observe negative correlations between phenotypic rates and clade age. We tested for such a relationship using phylogenetic generalized least-squares regression (Martins and Hansen 1997), finding no significant relationship between either clade age and size rate (Fig. 1A; $\beta = 0.001$; $P = 0.36$) or between clade age and shape rate (Fig. 1B; $\beta = 2.4 \times 10^{-5}$; $P = 0.46$).

Finally, if our phenotypic evolutionary rates reflect the rate at which clades accumulate morphological variance through time, then phenotypic disparity should be positively correlated with clade age. We estimated phenotypic disparity for each clade as the sum of squared Euclidean distances between measured specimens, standardized by the sample size. This measure of phenotypic disparity was significantly and positively correlated with clade age (Fig. 1C; phylogenetic generalized least-squares [PGLS] $\beta = 0.025$; $P = 0.05$). Because mean pairwise phylogenetic (patristic) distance between species within clades is highly correlated with clade age (Spearman's $r = 0.91$; $P < 0.001$), these results imply that older clades occupy a greater volume of phenotypic space than young clades. The PGLS results reported above (Fig. 1C) differ slightly from those reported in Adams et al. (2009), because here we modeled tip variances (e.g., the diagonal of the phylogenetic variance–covariance matrix) in our PGLS regressions by the total root-to-tip distance for each clade. Results reported in Adams et al. (2009) modeled tip variances as the root-to-crown age distance for each clade.

TESTING THE VALIDITY OF CR DIVERSIFICATION ESTIMATORS

For consistency throughout, we denote the per-lineage speciation rate by λ, the per-lineage extinction rate by μ, the net

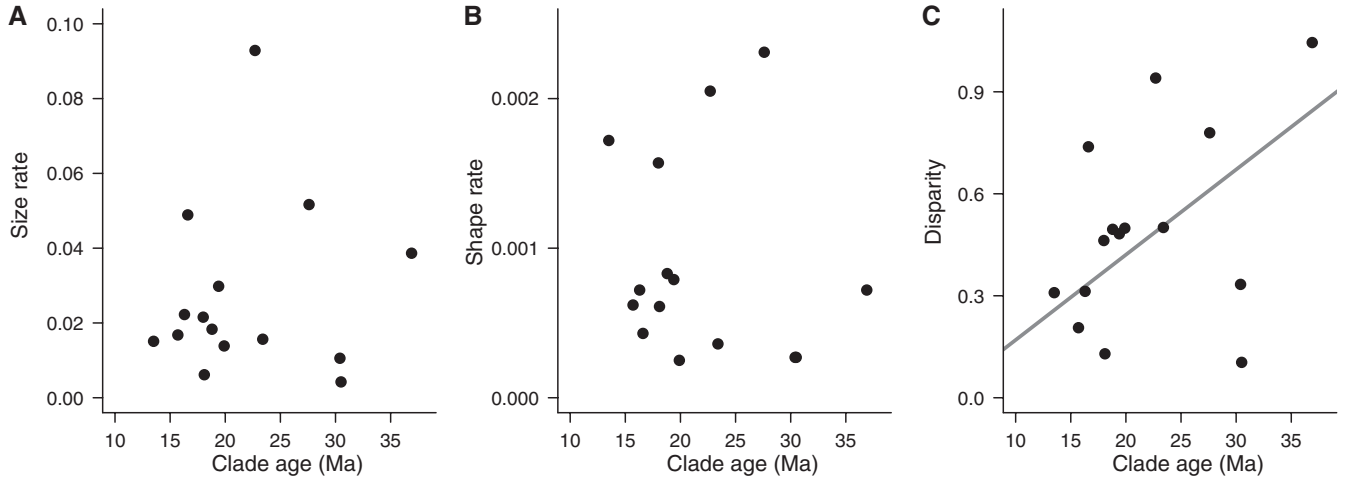


Figure 1. **Relationships between clade age and (A) rates of body size evolution, (B) rates of body shape evolution, and (C) phenotypic disparity. There is no relationship between clade age and either of the morphological evolutionary rates, but phenotypic disparity is significantly and positively associated with clade age.**

diversification rate ($\lambda - \mu$) by r, and the relative extinction rate (μ/λ) by ε. Wiens (2011) proposed that the correlation between clade species richness (N) and clade diversification rate ($\log(N)/t$ or variants thereof) could provide a simple test for the validity of CR diversification estimators. If this correlation is positive, then diversification rates provide some predictive ability with respect to clade richness, and CR estimators (Magallon and Sanderson 2001) retain explanatory power. However, there is a potential circularity with this test, as estimates of diversification rates are computed directly from the species richness values. As a consequence of this mathematical relationship, the correlation analyses may be compromised, as the association between species richness and clade diversification measures the relationship between a single variable (N) and a composite measure of itself ($\log(N)/t$) (see Atchley et al. (1976) for a similar discussion).

To determine whether this was the case for this test, we performed the following simulation. First, we simulated 50-clade datasets where we (1) sampled clade ages from a uniform distribution; (2) paired each of these ages with a species richness value sampled from a geometric distribution; (3) used the sampled ages and richness values to compute the net diversification rate, r, for each clade, using the method-of-moments estimator (Magallon and Sanderson 2001) under several relative extinction rates (ε); and (4) we computed the rank-order correlation between clade diversity and r for each simulated dataset. Thus, clade ages and species richness values in the simulations are sampled from uncorrelated distributions, and the species richness of each clade is not a function of any time-dependent process (by definition, the CR estimator describes a rate-limited process and requires that species richness in clades is some function of time). As expected, diversification rates and species richness are strongly correlated, despite the fact that no biological relationship between clade age and diversification rate was input into the simulation process (Fig. 2). As clade richness in simulations is sampled independently of clade age, a positive correlation implies type I error. Here, net diversification rates bear no relationship to clade diversity in any meaningful sense, yet based on the test of Wiens (2011) we would conclude that diversification rates bear some causal relationship to richness in a very high proportion of simulations.

AGE-DIVERSITY RELATIONSHIPS IN SALAMANDERS

For the 15 clades analyzed by Adams et al. (2009) there is no relationship between crown clade age and species richness (Spearman's $\rho = -0.15$, $P = 0.59$), suggesting that CR estimators may provide a poor explanation for observed patterns of species richness in clades and that diversity dependence may be constraining richness within clades (Ricklefs 2007; Rabosky 2010b). Although Rabosky (2009b) demonstrated that declining rates within clades could eliminate the relationship between clade age and species richness, it is also possible that this pattern could result from among-clade heterogeneity in diversification rates. This scenario was explicitly considered in Rabosky (2010b), where among-clade rate variation was modeled by assuming that clade diversification rates were drawn independently from a lognormal distribution. However, the Rabosky (2010b) model is explicitly nonphylogenetic: it assumes that there is no phylogenetic signal in the distribution of diversification rates across clades. In principle, however, such phylogenetic autocorrelation in rates could further weaken the expected relationship between clade age and species richness, perhaps eliminating it altogether.

To address this, we utilized a phylogenetic counterpart to the hierarchical model in Rabosky (2010b). We assume that the logarithm of the diversification rate across clades follows a

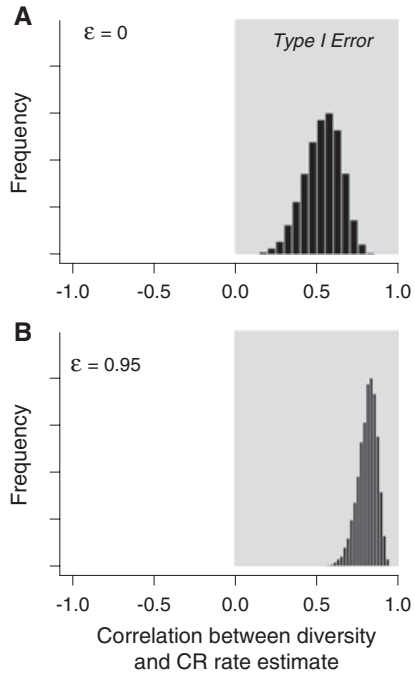


Figure 2. Correlations between net diversification rates and species richness expected when species richness and clade age are drawn independently from uncorrelated distributions devoid of biological significance. Net diversification rates were computed under low (A) and high (B) relative extinction rates. The test proposed by Wiens (2011) to assess the validity of constant-rate (CR) diversification estimators will almost always recover positive correlations when data lack any signal of a CR diversification process. Because CR diversification estimators are computed from species richness, they will generally be correlated with those richness values, even when diversity has not been generated under a time-dependent diversification process.

multivariate normal distribution with a mean equal to the value at the root node and a covariance structure specified by the phylogenetic variance–covariance matrix. This is simply a pairwise matrix containing sums of shared branch lengths for all species pairs. Diversification rates thus follow a multivariate lognormal distribution. This is similar to the model used to describe phylogenetic autocorrelation of molecular evolutionary rates along the branches of a phylogenetic tree (Thorne et al. 1998; Drummond et al. 2006). There are two hyperparameters in the model: the diversification rate at the root of the tree (θ), and a scalar multiplier of the phylogenetic variance–covariance matrix (ν). The probability density of observing a clade with n_i species, of age t_i, is given by

$$f(n_i|\theta, \nu, t_i) = \int_0^\infty \cdots \int_0^\infty f(n_i|r_i, t_i)\, f(r_i|\theta, \nu, r_1, r_2, \ldots r_N)\, dr_1, \ldots dr_N, \quad (1)$$

where r_i is the rate assigned to the ith terminal node. Computing the probability of observing even a single clade richness value given its age, as a function of hyperparameters θ and ν, requires integrating over all possible diversification rates at the tips of the tree.

We adopted a Bayesian approach to perform the integration in equation (1). This involves little more than specifying prior distributions on the hyperparameters (θ, ν) and approximating the joint posterior distribution of the hyperparameters using Markov Chain Monte Carlo (MCMC). The joint prior distribution is given by

$$f(\theta, \nu, r_1, \ldots r_N) = \int_0^\infty \cdots \int_0^\infty f(r_1, \ldots r_N|\theta, \nu)\, f(\theta)\, f(\nu)\, dr_1, \ldots dr_N, \quad (2)$$

where $f(\theta)$ and $f(\nu)$ are prior densities on the root rate and scale parameter, respectively. The joint posterior distribution is thus

$$f(\theta, \nu, r_1, \ldots r_N|n_1 \ldots n_N) = f(\theta, \nu, r_1, \ldots r_N) \times f(n_1, \ldots n_N|r_1, \ldots r_N) \quad (3)$$

and the data likelihood $f(n_1 \ldots n_N \mid r_1 \ldots r_N)$ is computed as in previous studies (Bailey 1964; Bokma 2003).

We assumed exponential prior distributions on both hyperparameters and used MCMC to summarize their joint posterior distribution. We ran separate MCMC analyses of 10^6 generations under six relative extinction rates ($\varepsilon = 0, 0.2, 0.4, 0.6, 0.8, 0.99$), sampling parameters every 1000 generations. For comparison, we also implemented a nonphylogenetic version of the hierarchical model described above (see Rabosky (2010b) for a non-Bayesian version). We simply assumed that net diversification rates for each clade are drawn independently from a lognormal distribution with (log) mean θ and variance ν. We refer to this latter model as the uncorrelated lognormal model.

POSTERIOR PREDICTIVE SIMULATION

If the CR estimators provide a meaningful summary of clade diversification histories, they must be able to explain the lack of relationship between clade age and species richness observed in salamanders (Rabosky 2010b). We conducted posterior predictive simulations for each combination of model and relative extinction rate to test whether phylogenetic and uncorrelated lognormal models of diversification rate variation can explain the observed distribution of species richness across salamander clades. We sampled hyperparameters θ and ν from their joint posterior distribution, then used these parameters to generate a sample of net diversification rates for each clade. For the phylogenetic model, this entailed drawing rates from a multivariate lognormal distribution with a covariance structure proportional to the observed phylogenetic variance–covariance matrix. We then simulated species richness values for each clade, given the observed clade age, the relative extinction rate, and the simulated diversification rate. For

each simulated dataset, we computed the rank-order correlation between clade age and log-transformed species richness.

SPECIATION RATES WITHIN CLADES

One possible explanation for a lack of relationship between clade age and species richness is that net diversification rates have slowed through time within clades, perhaps due to diversity dependence of speciation and/or extinction rates (Ricklefs 2007; Rabosky 2009a, 2010b; McInnes et al. 2011). The ecological mechanisms that might underlie diversity-dependent dynamics at the clade level remain poorly known and controversial (Rabosky 2010b; Wiens 2011), but substantial evidence for such dynamics comes from analyses of diversification patterns in species-level phylogenies (Phillimore and Price 2008; Rabosky and Lovette 2008a; Rabosky and Glor 2010; Etienne et al. 2011). If diversity dependence underlies the decoupling of age and species richness in salamanders, then we should observe a general slowdown in the rate of speciation through time within salamander clades.

We used the time-calibrated plethodontid phylogeny of 191 species from Adams et al. (2009) to test whether rates of species diversification have slowed through time within the 15 focal clades, as predicted if such slowdowns can explain the observed decoupling of age and species richness. Taxon sampling within the focal clades is incomplete, but a majority of clades (10/15) contain at least 50% of the known species (minimum: 32%; median: 58%). The analyses described below assume that taxon sampling within clades is effectively random with respect to phylogeny and that incompleteness reflects a lack of DNA samples for missing species rather than a targeted effort to include the most phylogenetically divergent subset of lineages.

To test for overall departures from a constant speciation model of clade diversification, we computed the γ-statistic (Pybus and Harvey 2000) for each clade. Negative values of this statistic imply an excess of early speciation events in the phylogeny relative to the expected number under a pure birth (constant rate) model of diversification. Due to incomplete taxon sampling, we generated null distributions of γ for each clade through simulation (Monte Carlo constant rate [MCCR] test; Pybus and Harvey 2000).

We then fitted time-varying models of speciation to each salamander clade using maximum likelihood (Rabosky and Lovette 2008b; Rabosky and Glor 2010; Morlon et al. 2011). Specifically, we modeled speciation rates within clades as

$$\lambda(t) = \lambda_0 e^{kt},$$

where λ_0 is the initial speciation rate, k is a rate change parameter, and t is elapsed time from the initial (crown) speciation event in the clade. This is a particularly useful model in the present context, as it can approximate a linear diversity-dependent change in the speciation rate through time (Quental and Marshall 2009). To visualize the pattern of lineage accumulation under the fitted models, we computed the expected number of lineages as

$$N(t) = 2\exp\left(\int_0^t \lambda(t)dt\right).$$

We accounted for incomplete sampling using the sampling model developed by Morlon et al. (2011) for the time-varying birth–death process. This approach enabled us to compute the likelihood of our phylogenetic data under any time-varying model of speciation, conditional on our assumed level of species sampling. We compared these fitted models to a simple constant rate speciation process in an Akaike information criterion (AIC) framework. We found that including extinction in the model did not appreciably improve our ability to model the data; moreover, estimated extinction rates tended toward zero for most clades. Given these results and general problems associated with the estimation of extinction from molecular phylogenies (Rabosky 2009c, 2010a), we present only results for the two-parameter time-varying speciation model and one-parameter CR speciation model.

CORRELATES OF PHENOTYPIC EVOLUTIONARY RATES

We used PGLS to assess the predictive ability of (1) CR diversification rate estimates and (2) log-transformed species richness in explaining the variation in phenotypic evolutionary rates across salamander clades. If the dynamics of species richness within clades is characterized by strong diversity dependence, then species richness itself emerges as an appropriate response variable in phylogenetic comparative analyses as an estimate of the total time-integrated diversification experienced by clades (Rabosky 2009b, 2010b). Alternatively, one can view the standing richness of clades as an estimate of their carrying capacity. However, there is no need to ascribe a particular causal mechanism to this relationship: we are ultimately interested in the factors that determine clade richness, and if clade richness is not a function of time, there is little justification for "correcting for time" by transforming species richness into a CR diversification rate estimate. Our PGLS models included a parameter for Pagel's lambda (denoted here by Λ), a scalar multiplier of the off-diagonal elements of the phylogenetic variance–covariance matrix that reflects the amount of phylogenetic signal in the residuals of the relationship between dependent and independent variables (Pagel 1997). We compared the relative importance of the two predictor variables (log-transformed richness and net diversification rate) for rates of both size and shape evolution using the Akaike information criterion. All analyses and simulations were conducted in the R statistical/programming environment. Source code and data underlying the analyses presented here have been deposited in the Dryad online data repository (doi:10.5061/dryad.vt41c78j).

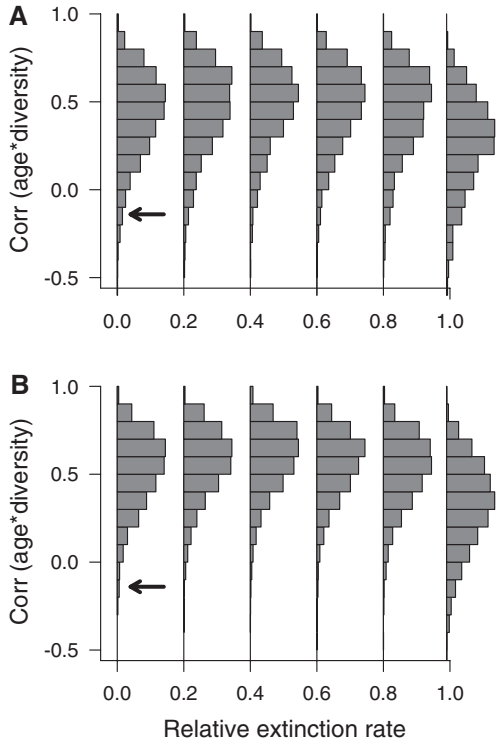


Figure 3. Expected rank-order correlation between clade age and species richness for plethodontid salamanders as a function of different relative extinction rates for (A) phylogenetic and (B) uncorrelated lognormal models of rate variation among clades. Arrow denotes observed age-diversity correlation for the salamander dataset. Both phylogenetic and nonphylogenetic models predict substantial positive relationships between clade age and species richness.

Results

We found that among-clade variation in net diversification rates is unlikely to explain the lack of relationship between clade age and species richness in plethodontid salamanders. Posterior predictive simulations under the uncorrelated and phylogenetic models of diversification rate variation indicate that strong positive correlations between age and species richness are expected for these data under all scenarios we considered that allowed rates to vary among clades (Fig. 3). For the phylogenetic model of rate variation (Fig. 3A), the probability of observing an age-diversity correlation equal to or less than that observed for salamanders (Spearman's $\rho = -0.15$) is less than 0.025 under all values of $\varepsilon \leq 0.8$, and is only somewhat more likely ($P = 0.076$) under the extreme case where speciation and extinction are approximately balanced ($\varepsilon = 0.99$). Under the uncorrelated lognormal model (Fig. 3B), the observed age-diversity correlation is even less likely ($P < 0.005$ for $\varepsilon \leq 0.8$; $P = 0.039$ for $\varepsilon = 0.99$). Our results imply that CR estimators of net diversification provide an inaccurate measure of clade diversification history for this group.

When we considered within-clade patterns of speciation, we found a striking signature of declining diversification rates across most plethodontid clades (Table 1). Observed γ-statistics were consistently less than zero, with most clades (11/15) showing at least marginally significant ($P < 0.10$) departures from a CR speciation process after accounting for incomplete taxon sampling. Similar results were obtained for model-based analyses of speciation dynamics, where 13/15 clades were characterized by $\Delta\text{AIC} > 0$ in favor of a time-varying speciation model. For each clade, the fitted time-varying models predict temporally declining rates of speciation and lineage accumulation (Fig. 4). Total AIC evidence across all 15 clades strongly favors a model with clade-specific and temporally declining rates of speciation, relative to a model with clade-specific but time-invariant rates of speciation (cumulative $\Delta\text{AIC} = 29.2$).

We found a significant positive relationship between log-transformed species richness and both phenotypic rate measures (Table 2; Fig. 5). However, we found no relationship between CR estimates of net diversification rate and rates of size or shape evolution, consistent with previous results (Adams et al. 2009). For rates of size and shape evolution, AIC scores favor log-transformed species richness over CR diversification estimates as a predictor of phenotypic rates (size rate: $\Delta\text{AIC} = 5.2$; shape rate: $\Delta\text{AIC} = 5.1$). CR estimates of net diversification rate given in Table 2 assume a relative extinction rate (μ/λ) of 0.45 (after Adams et al. 2009), but similar evidence favoring models with log-transformed richness was obtained when the relative extinction rate was treated as a free parameter to be estimated during PGLS analyses (size rate: $\Delta\text{AIC} = 5.3$; shape rate: $\Delta\text{AIC} = 4.3$). The relative extinction rate estimated from this analysis approached 1.0, but this estimate is likely to reflect model misspecification. Rabosky (2010b) documented severe statistical pathologies associated with the estimation of relative extinction rates from age and richness data when the assumptions of a time-homogeneous birth–death process are violated.

Discussion

These results indicate that log-transformed species richness is correlated with rates of phenotypic evolution in plethodontid salamanders and provide one of the first direct tests of the hypothesis that species diversification and morphological evolutionary rates can be coupled. By explicitly testing the validity of the CR diversification model, we found that CR estimators do not provide a valid summary of clade diversification histories in salamanders. As species richness in clades is not a function of time-for-diversification, it is not appropriate to "correct" for clade age by computing CR estimates of net diversification rates for each clade. Consistent with this possibility, we found that species richness itself is a better predictor of phenotypic evolutionary rates than CR estimates of net diversification (Table 2).

Table 1. Diversification through time in plethodontid salamander clades. Clade numbers correspond to those in Adams et al. (2009). MCCR *P*-value is the one-tailed probability of the observed γ-statistic under the null hypothesis of constant speciation through time. AIC_{CR} and AIC_{VR} are AICs for the constant-rate (CR) and variable-rate models of speciation, respectively.

Clade	Species in clade/ species in tree	γ	MCCR *P*-value	AIC_{CR}	AIC_{VR}	ΔAIC
(1) *Desmognathus* and *Phaeognathus*	37/12	–1.9	0.16	87.08	88.64	–1.56
(2) *Aneides*	6/5	–1.37	0.03	36.47	34.69	1.78
(3) Western *Plethodon*	9/6	–1.4	0.07	44.54	42.14	2.4
(4) *P. cinereus* group	10/7	–1.53	0.05	44.4	43.75	0.65
(5) *P. wehrlei-welleri* group	7/6	–0.99	0.08	39.46	38.96	0.5
(6) *P. glutinosus* group	28/18	–2.48	0.02	109.95	105.74	4.21
(7) *Gyrinophilus, Pseudotriton*, and *Stereochilus*	7/4	–2.17	<0.01	27.47	17.72	9.75
(8) *Eurycea*	36/17	–0.92	0.42	118.87	120.08	–1.21
(9) *Nototriton*	13/5	–0.37	0.45	28.59	29.97	–1.38
(10) *Oedipina*	25/10	–1.74	0.11	63.42	62.09	1.33
(11) *Chiropterotriton*	12/7	–2.47	<0.01	45.19	38.49	6.7
(12) *Pseudoeurycea* clade	51/32	–2.03	0.07	215.13	214.47	0.66
(13) *Bolitoglossa*, subgenus *Eladinea*	46/15	–2.69	0.04	88.47	88.15	0.32
(14) *Bolitoglossa*, subgenera *Magnadigita, Oaxakia*, and *Pachymandra*	25/19	–2.65	<0.01	121.97	117.86	4.11
(15) *Bolitoglossa*, subgenera *Bolitoglossa, Mayamandra*, and *Nanotriton*	17/10	–1.83	0.06	64.01	63.03	0.98

The simple Brownian motion estimates of phenotypic evolutionary rates we consider here potentially suffer from the same limitations as CR estimators of species diversification rates. For example, constraints on phenotypic divergence can lead to negative correlations between phenotypic evolutionary rates and clade age. If a set of clades occupy similar volumes of morphological space but vary substantially in age, then we might estimate low rates of evolution for old clades and fast rates for young clades. Negative correlations between phenotypic evolutionary rates and clade age (or timescale of measurement) have been reported in several previous studies (Gingerich 2001; Ackerly 2009), suggesting the possibility that the phenotypic rates we consider here might be confounded with clade age. However, our analyses of the relationship between clade age, phenotypic rates, and phenotypic disparity suggest that these rates are not confounded by clade age (Fig. 1; see Materials and Methods).

It is possible that error in the estimation of clade age could weaken or even eliminate a "true" positive correlation between age and diversity. We suggest that this is unlikely for several reasons. First, we find that phenotypic disparity increases with clade age, as expected under a model of trait evolution by Brownian motion (Fig. 1C). There is no reason to expect this result if estimated clade ages are only weakly correlated with true clade ages. Second, through our analysis of species-level diversification patterns, we have provided independent evidence that speciation rates have declined through time in most clades. Such temporal decelerations in diversification rates can lead to a decoupling between age and diversity at the clade level (Rabosky 2009b). In a more general sense, we note that fossil-based clade ages are sometimes uncorrelated with species richness (Magallon and Sanderson 2001; Rabosky 2009b), further supporting the notion that this is a real biological phenomenon.

A number of causal mechanisms may underlie the patterns we have documented in this study. One interpretation of these results is that clades with higher rates of phenotypic evolution diversify more than low-rate clades. If there are strong diversity-dependent controls on species richness within clades, then clades with higher phenotypic rates may occupy increasingly broad regions of ecological space. If the number of species is determined by the size of the "adaptive zone" (Simpson 1953) occupied by the clade, and if the overall size of the adaptive zone is itself a function of the evolvability or versatility of the clade (Vermeij 1973a; Liem and Osse 1975), then species-rich clades should be characterized by higher rates of ecological innovation, which may in turn be approximated by the phenotypic diversification rates we measured in salamanders. This assumes that the rates of phenotypic evolution we have measured are associated with ecological diversification, and additional data are needed to test this hypothesis.

However, we cannot yet determine whether phenotypic evolutionary rates may be causally related to species richness. One

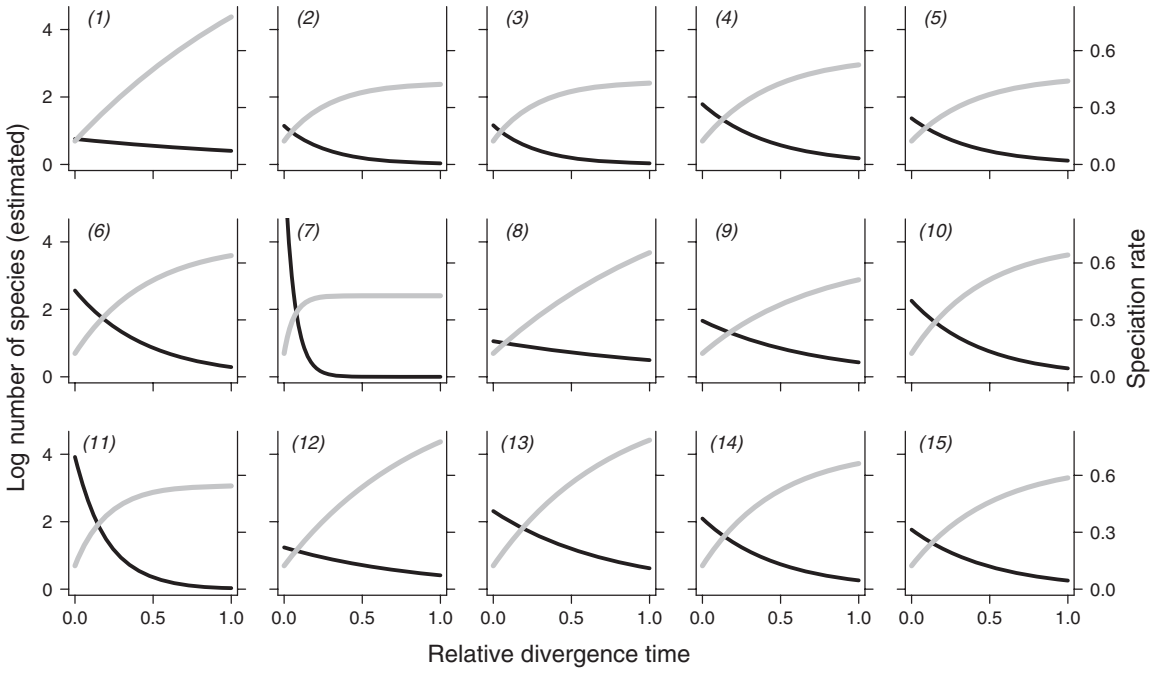


Figure 4. Maximum likelihood estimates of the rate of speciation through time (black lines) for 15 plethodontid salamander clades. Gray lines denote estimated log-transformed diversity through time under the fitted model. Plot numbers correspond to clade indices in Table 1.

Table 2. Statistical summary of PGLS regressions between two measures of species diversification (net diversification rate or log-transformed species richness) and morphological evolutionary rates. Δ_i is the AIC weight for the model, and Λ ("lambda") is the maximum likelihood estimate of Pagel's (1997) parameter for phylogenetic signal.

Model	AIC	Δ_i	Λ	β	t	P
Size rate by net diversification rate	–66.1	0.07	0	0.105	0.73	0.479
Size rate by species richness	–71.3	0.93	0.36	0.017	2.057	**0.031**
Shape rate by net diversification rate	–173.2	0.07	1	0.0044	1.13	0.279
Shape rate by species richness	–178.3	0.93	1	0.0005	2.979	**0.02**

Statistically significant results are in bold.

alternative interpretation of these results is that species richness itself drives higher rates of phenotypic evolution. This might be expected if ecological character displacement is more common in species-rich clades, perhaps due to denser packing in geographic and ecological space. Competitive interactions are well known to have shaped patterns of community composition (Adams 2007) and morphological variation in plethodontid communities (Adams and Rohlf 2000; Adams 2004, 2010). However, causality in this scenario is also unclear: it is also possible that lineages with greater capacity for ecological character displacement will contain more species, particularly if species persistence and/or speciation itself is facilitated by ecological divergence from other species. This is especially relevant when considering the effects of range expansions on speciation and species persistence. Geographic range expansions may be a critical part of "successful" speciation, but they may require that recently separated allospecies undergo ecological or morphological divergence before sympatry is possible (Rundell and Price 2009).

The lack of correlation between clade age and species richness suggests the intriguing possibility of diversity-dependent control of clade size in salamanders, consistent with previous evidence for declining speciation rates observed in several plethodontid subclades (Kozak et al. 2006; Kozak and Wiens 2010). Our finding of parallel declines in the rate of speciation through time within plethodontid clades provides further support for this hypothesis (Table 1; Fig. 4). Previous studies have speculated that diversity-dependent declines in net speciation rates might underlie the decoupling of age and species richness reported in other groups (Ricklefs and Renner 1994; Ricklefs 2007; Rabosky 2009a). To our knowledge, this is the first study to demonstrate correspondence of within-clade patterns of speciation through time and age-diversity relationships at the clade level.

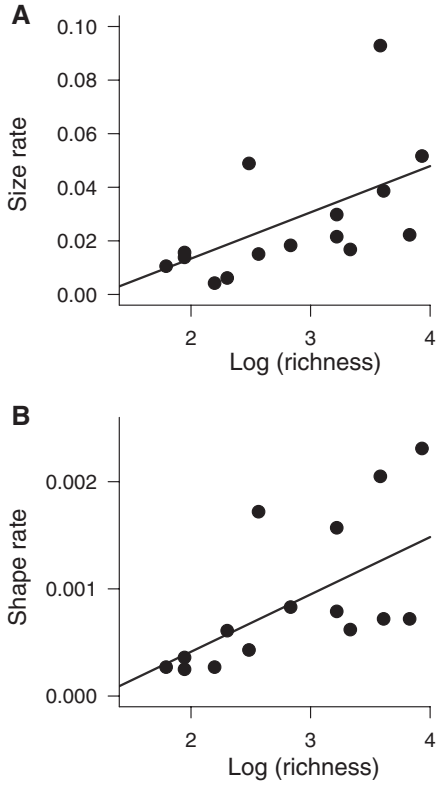


Figure 5. Relationship between rates of morphological evolution and total species diversification (log-transformed richness) for 15 clades of plethodontid salamanders. (A) Relationship between rate of body size evolution and species richness. (B) Relationship between rate of shape evolution and species richness. Both phenotypic evolutionary rates are significantly and positively associated with species richness (size rate: $P = 0.033$; shape rate: $P = 0.019$).

We are only beginning to understand the population ecological mechanisms that might define a macroevolutionary "adaptive zone" or "carrying capacity" at the clade level. Such a carrying capacity is clearly more than the simple sum of local-scale niches that are occupied by species within a clade and potentially includes geographic opportunities for speciation (Kisel and Barraclough 2010), the effects of species interactions on range size and range expansions (Price and Kirkpatrick 2009), and feedbacks between local and regional diversity. A lack of relationship between clade age and species richness does not constitute a strong test for diversity dependence. However, given that we have also found a signal of declining diversification rates within salamander clades, diversity dependence remains an important candidate process to explain this pattern. If the decoupling between age and species richness is merely an artifact of the way higher taxa are delimited (Rabosky 2010b), then we would not expect to observe (1) correlations between phenotypic covariates of putative ecological significance (shape and size rates) and species diversification, and (2) a consistent signal of declining speciation through time within clades (Fig. 4). Regardless, more effective tests of the mechanisms that underlie the age-diversity relationship in salamanders and other taxa will require greater integration of phylogenetic, ecological, geographic, and paleontological data.

A CAUTION FOR MODEL-BASED INFERENCE

Using an AIC framework, we found that log-transformed species richness is a better predictor of both size and shape evolutionary rates than CR estimates of net diversification rate (Table 2). However, although AIC comparisons provide corroborative evidence favoring one model over another, in some instances model selection can be positively misleading; for example, if the independent variable (diversification rate or richness) and dependent variable (ecological or phenotypic covariate) are related by virtue of secondary correlations with some unknown factor. This is especially likely in the analyses of evolutionary rates, where time can potentially confound both the predictor and response variables. Consider a simple scenario where clade richness is independent of clade age, perhaps due to diversity-dependent regulation of speciation and extinction. CR estimates of net diversification for such clades may be devoid of biological meaning but will nonetheless show negative correlations with clade age (Rabosky 2009a); they will thus be correlated with any time-dependent ecological or phenotypic covariates.

This is a serious concern, partly because many potential correlates of species diversification show real or artifactual correlations with the timescale over which they are measured (including phenotypic evolutionary rates [Kurten 1959; Gingerich 2001; Ackerly 2009] and molecular evolutionary rates [Ho et al. 2011]). These problems are exacerbated if researchers interpret correlations between "net diversification rates" and ecological covariates as evidence that those rates are causal with respect to species richness. Whether such rates can potentially explain species richness must be addressed independently, as we have done here for salamanders.

Summary

The results presented here indicate that assumptions about models of diversity regulation can have profound consequences for interpreting macroevolutionary patterns. Adams et al. (2009) estimated salamander diversification rates under the assumption that diversity has increased continuously through time, finding no correlation between diversification rates and rates of phenotypic evolution. By applying new tools for modeling diversification dynamics within clades, we found that species richness is itself a more appropriate variable in "downstream" phylogenetic comparative analyses. Species richness across 15 clades of plethodontid salamanders is correlated with rates of body size and shape evolution, consistent with the hypothesis that phenotypic evolutionary rates promote species diversification. Although we cannot yet

establish the direction of causality, our results are consistent with a number of models that postulate coupling between patterns of phenotypic evolution and species diversification.

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LITERATURE CITED

Ackerly, D. 2009. Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. Proc. Nat. Acad. Sci. U.S.A. 106:19699–19706.

Adams, D. C. 2004. Character displacement via aggressive interference in appalachian salamanders. Ecology 85:2664–2670.

———. 2007. Organization of Plethodon salamander communities: guild-based community assembly. Ecology 88:1292–1299

———. 2010. Parallel evolution of character displacement driven by competitive selection in terrestrial salamanders. BMC Evol. Biol. 10:1–10.

Adams, D. C., and F. J. Rohlf. 2000. Ecological character displacement in Plethodon: biomechanical differences found from a geometric morphometric study. Proc. Nat. Acad. Sci. U.S.A 97:4106–4111.

Adams, D. C., C. M. Berns, K. H. Kozak, and J. J. Wiens. 2009. Are rates of species diversification correlated with rates of morphological evolution? Proc. R. Soc. Lond. B 276:2729–2738.

Alfaro, M. E., F. Santini, C. Brock, H. Alamillo, A. Dornburg, D. L. Rabosk, G. Carnevale, and L. J. Harmon. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. Proc. Nat. Acad. Sci. U.S.A. 106:13410–13414.

Alroy, J. 2008. The dynamics of origination and extinction in the marine fossil record. Proc. Nat. Acad. Sci. U.S.A. 105:11536–11542.

Atchley, W. R., C. T. Gaskins, and D. Anderson. 1976. Statistical properties of ratios .1. Empirical results. Syst. Zool. 25:137–148.

Bailey, N. T. J. 1964. The elements of stochastic processes with applications to the natural sciences. Wiley, New York.

Bokma, F. 2003. Testing for equal rates of cladogenesis in diverse taxa. Evolution 57:2469–2474.

Drummond, A. J., S. W. Y. Ho, M. J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol. 4: 699–710.

Eastman, J. M., M. E. Alfaro, P. Joyce, A. L. Hipp, and L. J. Harmon. 2011. A novel comparative method for identifying shifts in the rate of character evolution on trees. Evolution 65:3578–3589.

Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. Pp. 182–215 *in* T. J. M. Schopf, ed. Models in paleobiology. Freeman Cooper, San Francisco.

Etienne, R. S., B. Haegeman, T. Stadler, T. Aze, P. N. Pearson, A. Purvis, and A. B. Phillimore. 2011. Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. Proc. R. Soc. Lond. B doi: 10.1098/rspb.2011.1439.

Gingerich, P. D. 2001. Rates of evolution on the time scale of the evolutionary process. Genetica 112–113:127–144.

Harmon, L. J., J. A. Schulte, A. Larson, and J. B. Losos. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. Science 301:961–964.

Heard, S. B., and D. L. Hauser. 1995. Key evolutionary innovations and their ecological mechanisms. Hist. Biol. 10:151–173.

Ho, S. W. Y., R. lanfear, L. Bromham, M. J. Phillips, J. Soubrier, A. G. Rodrigo, and A. Cooper. 2011. Time-dependent rates of molecular evolution. Mol. Ecol. 20:3087–3101.

Kisel, Y., and T. G. Barraclough. 2010. Speciation has a spatial scale that depends on levels of gene flow. Am. Nat. 175:316–334.

Kozak, K. H., and J. J. Wiens. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. Ecol. Lett. 13:1378–1389.

Kozak, K. H., D. W. Weisrock, and A. Larson. 2006. Rapid lineage accumulation in a non-adaptive radiation: phylogenetic analysis of diversification rates in eastern North American woodland salamanders (Plethodontidae: Plethodon). Proc. R. Soc. Lond. B 273:539–546.

Kozak, K. H., R. W. Mendyk, and J. J. Wiens. 2009. Can parallel diversification occur in sympatry? Repeated patterns of body-size evolution in coexisting clades of North American salamanders. Evolution 63:1769–1784.

Kurten, B. 1959. Rates of evolution in fossil mammals. Cold Spring Harb. Symp. Quant. Biol. 24:205–215.

Liem, K. F., and J. W. M. Osse. 1975. Biological versatility, evolution, and food resource exploitation in African cichlid fishes. Am. Zool. 15: 427–454.

Magallon, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. Evolution 55:1762–1780.

Mahler, D. L., L. J. Revell, R. E. Glor, and J. B. Losos. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of greater Antillean anoles. Evolution 64:2731–2745.

Martin, C. H., and P. C. Wainwright. 2011. Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of Cyprinodon pupfish. Evolution 65:2197–2212.

Martins, E. P., and T. A. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am. Nat. 149:646–667.

McInnes, L. M., C. D. L. Orme, and A. Purvis. 2011. Detecting shifts in diversity limits from molecular phylogenies: what can we know? Proc. R. Soc. Lond. B 278:3294–3302.

McPeek, M. A. 2008. Ecological dynamics of clade diversification and community assembly. Am. Nat. 172:E270–E284.

McPeek, M. A., L. Shen, J. Z. Torrey, and H. Farid. 2008. The tempo and mode of 3-dimensional morphological evolution in male reproductive structures. Am. Nat. 171:E158–E178.

Morlon, H., T. L. Parsons, and J. B. Plotkin. 2011. Reconciling molecular phylogenies with the fossil record. Proc. Natl. Acad. Sci. U.S.A. 108:16327–16332.

Pagel, M. 1997. Inferring evolutionary processes from phylogenies. Zool. Scripta 26:331–348.

Parent, C. E., and B. J. Crespi. 2009. Ecological opportunity in adaptive radiation of Galapagos endemic land snails. Am. Nat. 174:898–905.

Phillimore, A. B., and T. D. Price. 2008. Density dependent cladogenesis in birds. PLoS Biol. 6:e71.

Price, T. D., and M. Kirkpatrick. 2009. Evolutionarily stable range limits set by interspecific competition. Proc. R. Soc. Lond. B 276:1429–1434.

Purvis, A. 2004. Evolution – How do characters evolve? Nature 432:1.

Pybus, O. G., and P. H. Harvey. 2000. Testing macro-evolutionary models using incomplete molecular phylogenies. Proc. R. Soc. Lond. B 267:2267–2272.

Pyron, R. A., and F. T. Burbrink. 2011. Extinction, ecological opportunity, and the origins of global snake diversity. Evolution 66:163–178.

Quental, T. B., and C. R. Marshall. 2009. Extinction during evolutionary radiations: reconciling the fossil record with molecular phylogenies. Evolution 63:3158–3167.

Rabosky, D. L. 2009a. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. Ecol. Lett. 12:735–743.

———. 2009b. Ecological limits on clade diversification in higher taxa. Am. Nat. 173:662–674.

———. 2009c. Heritability of extinction rates links diversification patterns in molecular phylogenies and fossils. Syst. Biol. 58:629–640.

———. 2010a. Extinction rates should not be estimated from molecular phylogenies. Evolution 64:1816–1824.

———. 2010b. Primary controls on species richness in higher taxa. Syst. Biol. 59:634–645.

Rabosky, D. L., and R. E. Glor. 2010. Equilibrium speciation dynamics in a model adaptive radiation of island lizards. Proc. Natl. Acad. Sci. U.S.A. 107:22178–22183.

Rabosky, D. L., and I. J. Lovette. 2008a. Density-dependent diversification in North American wood warblers. Proc. R. Soc. Lond. B 275:2363–2371.

———. 2008b. Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? Evolution 62:1866–1875.

Raup, D. M. 1985. Mathematical models of cladogenesis. Paleobiology 11:42–52.

Raup, D. M., S. J. Gould, T. J. M. Schopf, and D. Simberloff. 1973. Stochastic models of phylogeny and evolution of diversity. J. Geol. 81:525–542.

Ricklefs, R. E. 2004. Cladogenesis and morphological diversification in passerine birds. Nature 430:338–341.

———. 2006. Time, species, and the generation of trait variance in clades. Syst. Biol. 55:151–159.

———. 2007. Estimating diversification rates from phylogenetic information. Trends Ecol. Evol. 22:601–610.

Ricklefs, R. E., and S. S. Renner. 1994. Species richness within families of flowering plants. Evolution 48:1619–1636.

Rosenzweig, M. L. 1975. On continental steady states of species diversity. Pp. 121–140 *in* M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Belknap, Cambridge, U.K.

Rundell, R. J., and T. D. Price. 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. Trends Ecol. Evol. 124:394–399.

Sepkoski, J. J. 1978. A kinetic model of Phanerozoic taxonomic diversity I. Analysis of marine orders. Paleobiology 4:223–251.

Simpson, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York.

Slater, G. J., S. A. Price, F. Santini, and M. E. Alfaro. 2010. Diversity versus disparity and the radiation of modern cetaceans. Proc. R. Soc. Lond. B 277:3097–3104.

Thorne, J. L., H. Kishino, and I. S. Painter. 1998. Estimating the rate of evolution of the rate of molecular evolution. Mol. Biol. Evol. 15:1647–1657.

Vamosi, J. C., and S. M. Vamosi. 2010. Key innovations within a geographical context in flowering plants: towards resolving Darwin's abominable mystery. Ecol. Lett. 13:1270–1279.

Venditti, C., A. Meade, and M. Pagel. 2011. Multiple routes to mammalian diversity. Nature 479:393–396.

Vermeij, G. J. 1973a. Adaptation, versatility, and evolution. Syst. Zool. 22:466–477.

———. 1973b. Biological versatility and earth history. Proc. Natl. Acad. Sci. U.S.A. 70:1936–1938.

Walker, T. D., and J. W. Valentine. 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. Am. Nat. 124:887–899.

Weir, J. T. 2006. Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. Evolution 60:842–855.

Wiens, J. J. 2007. Global patterns of diversification and species richness in amphibians Am. Nat. 170:S86–S106.

———. 2011. The causes of species richness patterns across space, time, and clades and the role of "ecological limits". Q. Rev. Biol. 86:75–96.

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