

# EXTINCTION, ECOLOGICAL OPPORTUNITY, AND THE ORIGINS OF GLOBAL SNAKE DIVERSITY

R. Alexander Pyron<sup>1,2</sup> and Frank T. Burbrink<sup>3,4,5</sup>

<sup>1</sup>*Department of Biological Sciences, The George Washington University, 2023 G St. NW, Washington, DC 20052*

<sup>2</sup>*E-mail: rpyron@colubroid.org*

<sup>3</sup>*Department of Biology, The Graduate School and University Center, The City University of New York, 365 5th Avenue, New York, NY 10016*

<sup>4</sup>*Department of Biology, The College of Staten Island, The City University of New York, 2800 Victory Boulevard, Staten Island, NY 10314*

<sup>5</sup>*E-mail: frank.burbrink@mail.csi.cuny.edu*

Received November 14, 2010

Accepted June 20, 2011

Data Archived: Dryad doi:10.5061/dryad.63kf4

Snake diversity varies by at least two orders of magnitude among extant lineages, with numerous groups containing only one or two species, and several young clades exhibiting exceptional richness (>700 taxa). With a phylogeny containing all known families and subfamilies, we find that these patterns cannot be explained by background rates of speciation and extinction. The majority of diversity appears to derive from a radiation within the superfamily Colubroidea, potentially stemming from the colonization of new areas and the evolution of advanced venom-delivery systems. In contrast, negative relationships between clade age, clade size, and diversification rate suggest the potential for possible bias in estimated diversification rates, interpreted by some recent authors as support for ecologically mediated limits on diversity. However, evidence from the fossil record indicates that numerous lineages were far more diverse in the past, and that extinction has had an important impact on extant diversity patterns. Thus, failure to adequately account for extinction appears to prevent both rate- and diversity-limited models from fully characterizing richness dynamics in snakes. We suggest that clade-level extinction may provide a key mechanism for explaining negative or hump-shaped relationships between clade age and diversity, and the prevalence of ancient, species-poor lineages in numerous groups.

**KEY WORDS:** Clade size, diversification rates, diversity regulation, ecological limits, extinction, global biodiversity, snakes, speciation.

Many taxonomic groups comprise clades with vast disparities in species richness, even among closely related lineages in adjacent areas (Fischer 1960; Rosenzweig 1995). A prime example is Lepidosauria: tuataras are represented by only two extant species, while their sister group Squamata (lizards and snakes) contains nearly 9000 species (Vitt and Caldwell 2009). Many hypotheses have been proposed to explain these patterns, although the underlying causes are still unclear for most groups (Rosenzweig 1995;

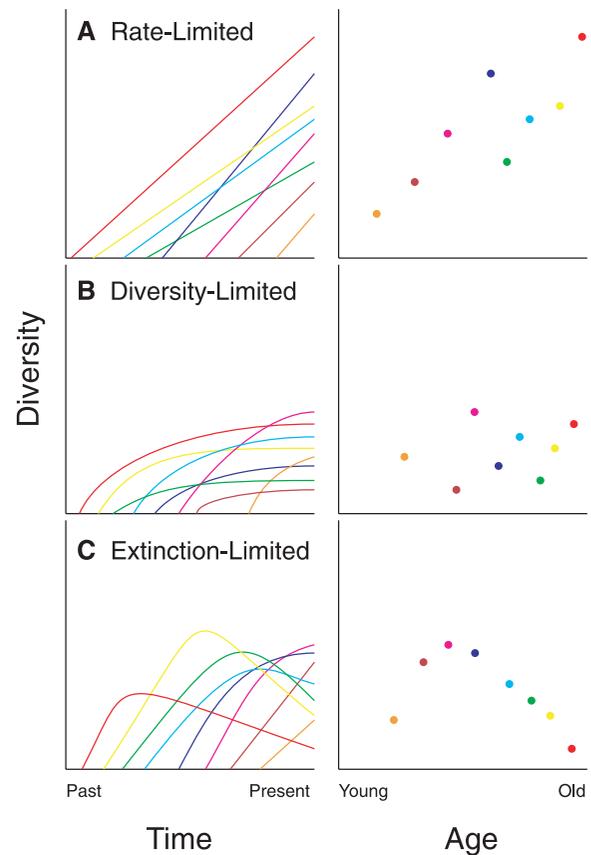
Mittelbach et al. 2007; Butlin et al. 2009). Species richness is generally attributed either to clade age and diversification rate (Magallón and Sanderson 2001; Stephens and Wiens 2003; Cardillo et al. 2005; McPeck and Brown 2007), or primary controls on diversity, such as ecological limits on clade size, constraining total diversity in clades or species richness in areas through a variety of potential mechanisms (Levinton 1979; Walker and Valentine 1984; Rabosky 2009a,b, 2010a). Explaining variation

in diversity has typically relied heavily on this small group of models, potentially limiting our ability to adequately characterize these processes through time (see Gould et al. 1977; Nee et al. 1994).

When diversity is modeled as a function of speciation and extinction using a birth–death model, a geometric distribution of clade sizes results (Ricklefs 2007). Such a rate-limited process produces a positive relationship between clade age and diversity (Rabosky 2009a). This general mechanism has been used to explain patterns in biodiversity at numerous scales (Stephens and Wiens 2003; Wiens and Donoghue 2004; McPeck and Brown 2007). However, many groups lack a positive age–diversity relationship (Ricklefs 2006, 2007) prompting some authors to suggest that clade size may be diversity regulated (Ricklefs et al. 2007; Rabosky 2009a), potentially involving ecological factors such as area or energy limiting the total number of species that can exist (see Losos and Schluter 2000; Evans et al. 2005; Hurlbert and Jetz 2010). Recently developed models account for such ecological controls on diversity independent of clade age by comparing rate-limited process to total time-integrated speciation ( $\Omega$ ; Rabosky 2010a).

Although many ecological or temporal circumstances may impact diversification in a group, species richness in clades is always controlled by two and only two processes: speciation and extinction. Thus, any other biotic or abiotic factor resulting in any impact on diversity must therefore act by affecting one of those two processes, bringing both rates into equilibrium to yield a steady number of taxa through time (see Wiens 2011). Additionally, neither rate- nor diversity-limited processes typically account for deterministic extinction (where extinction exceeds speciation), despite its apparent prevalence (i.e., the possible deterministic extinction of entire clades) in the fossil record (e.g., Sloss 1950; Van Valen 1975; see Raup 1985). Such a process would lead to a hump-shaped or decreasing distribution of diversity through time (Fig. 1). A negative relationship between clade age and diversity has been noted in several groups (see Rabosky 2009a). Deterministic extinction could also account for the prevalence of old, depauperate lineages in many groups (see also Strathmann and Slatkin 1983; Jablonski 2002).

Thus, the assumptions made by both rate- and diversity-limited processes, that a lineage will either continue to diversify or maintain a constant richness through time, respectively, seem unlikely. For example, young clades may show a positive age–diversity relationship (e.g., New World [NW] geckos; Gamble et al. 2011). However, it seems likely that after a sufficient amount of time has passed (e.g., the “half life” [hL] of a clade; see Raup 1985), a lineage will either decline to extinction (Foote 2007), or diverge into new biogeographic or ecomorphological adaptive zones (Simpson 1953), thus becoming multiple daughter clades.



**Figure 1.** Cartoon illustration of the different expectations of species richness through time and the age–diversity relationship under a rate-limited process (A), diversity-limited process (B), and an extinction-limited process (C). These models are tested empirically for the snakes (Table 2).

Support for these patterns, particularly the tendency for lineages to exhibit deterministic extinction, is found for numerous taxa in the fossil record (e.g., Gould et al. 1977; Foote et al. 2007). Thus, over time, we might expect higher taxa (e.g., groups of biogeographically or ecomorphologically distinct species) to either (1) undergo an initial period of diversification and subsequently decline toward group extinction (e.g., ornithischian dinosaurs; the apparent fate of tuataras and coelocanths), or (2) diverge sufficiently to be considered “new” lineages, occupying distinct biogeographic provinces or ecomorphological zones (e.g., lizards and snakes, saurischian dinosaurs and birds).

Here, we examine patterns of diversity in snakes and test several hypotheses regarding speciation, extinction, and primary controls on clade size. Snakes represent a large radiation of terrestrial vertebrates with an extremely large distribution, comprising nearly 3500 species distributed across every continent except Antarctica (Vitt and Caldwell 2009; Burbrink and Crother 2011). Extant snakes originated in the late Jurassic or early Cretaceous, and the largest group, the superfamily Colubroidea, diversified

in the Cenozoic (Burbrink and Pyron 2008; Vidal et al. 2009). Some lineages, such as the subfamily Dipsadinae, contain over 700 species (22% of all snakes), whereas others (e.g., Aniliidae, Loxocemidae, Calabariidae, etc.) contain only one known species (Vitt and Caldwell 2009; Burbrink and Crother 2011; Pyron et al. 2011). In addition to the extant snakes, numerous extinct families are known worldwide throughout the Mesozoic and Cenozoic, many having attained substantial diversity (Rage 1984; Holman 2000).

For the first time, we present a phylogeny containing representatives of all known extant families and subfamilies of snakes based on data from 27 independent loci. We use the MEDUSA algorithm (Alfaro et al. 2009) to identify lineages that appear to have experienced significant shifts in diversification rate based on their age and estimates of current diversity while using a birth–death model that permits multiple rate shifts across the tree. We then use clade-based methods to determine if species richness in snakes can be explained by simple models of diversification. We use estimated rates of diversification to generate confidence limits on clade size through time under a birth–death model (Magallón and Sanderson 2001) to identify clades with more or less species than expected. We then test for a relationship between clade age and extant diversity. Finally, we fit a series of models to determine whether the diversity of snakes is best explained by rate-limited or diversity-limited processes (Rabosky 2010a), and derive a model that incorporates clade-level extinction after an initial period of diversification.

Neither rate- nor diversity-limited processes can fully explain diversity patterns in extant snakes. For several colubroid groups, colonization of the NW or the evolution of advanced venom-delivery systems and toxic salivary components may have facilitated extraordinary diversification. However, although increasing diversification rates may be responsible for the extraordinary species richness of several relatively young lineages, this cannot explain the presence of numerous ancient clades with only one or a few species. The inability of both rate-based and diversity-regulated models to adequately capture diversity dynamics may be related to their failure to consider extinction as a key force in diversification and as the ultimate fate of both species and clades (e.g., Van Valen 1975; Gould et al. 1977; Foote et al. 2007; Fig. 1). Diversification analyses using molecular phylogenies typically focus only on diversification rates in extant taxa, representing a vanishingly small fraction of the billions of species that have ever existed. Thus, extinction has clearly had a massive but often overlooked impact on both current and historical diversity patterns. Despite the difficulty of studying extinction with molecular phylogenies (e.g., Rabosky 2010b), we suggest that it should play a much larger role in the interpretation of species richness patterns in both clades and areas.

## Materials and Methods

### SEQUENCE DATA

We combined several existing DNA datasets (Vidal and Hedges 2002; Lawson et al. 2004; Gower et al. 2005; Vidal et al. 2007, 2008, 2009, 2010; Wiens et al. 2008) to produce a matrix including one representative from every known, extant family and subfamily of snakes, for a total of 40 terminal taxa (Wiens et al. 2008; Pyron et al. 2011), plus Varanidae as an outgroup (Vidal et al. 2009; Wiens et al. 2010). In most cases, these 40 higher taxa were represented by sequences from a single species, but in nine cases (Aparallactinae, Atractaspididae, Leptotyphlopidae, Pareatidae, Pseudoxenodontinae, Tropidophiidae, Typhlopidae, Uropeltidae, and Varanidae), we used sequences from multiple species in the same genus to create the terminal “taxon” to increase the total number of genes represented for that taxon. We exhaustively surveyed the available data, so that the species chosen for each terminal were the ones with the greatest number of loci, such that the percentage identity of each terminal was as high as possible. This approach has been shown to be robust under empirical conditions (Campbell and Lapointe 2009, 2010). The final matrix contained sequence data totaling up to 18,924 bp from 29 genes for 41 taxa (terminal taxa, genes, and accession numbers are in Appendix S1; the matrix and trees are available in Dryad repository (doi:10.5061/dryad.63kf4), with an average of 20 genes sampled per taxon. The matrix was 67% complete in terms of the number of total gene sequences present. However, for some rare taxa (e.g., Anomochilidae, Xenophiidae, and Scaphiodontophiinae), we obtained only one or a few genes (Lawson et al. 2004; Gower et al. 2005; Pyron et al. 2011), as these groups are known from only a few specimens.

### PHYLOGENETIC ANALYSES

We estimated phylogeny and divergence times simultaneously using an uncorrelated lognormal relaxed-clock model in the program BEASTv1.6.1 (Drummond and Rambaut 2007). The matrix was partitioned by gene, with the optimal model for each gene determined using jModeltest (Posada 2008). Although previous studies have found codon-position-specific partitions to yield a better fit for at least 20 of the 27 protein-coding genes (Wiens et al. 2008), this resulted in apparent overparameterization with this dataset, causing problems with Markov chain Monte Carlo (MCMC) convergence and the ability to properly identify parameters (see Rannala 2002) in preliminary analyses. However, lack of codon partitioning has been shown to have a small impact on divergence-time estimates in similar multilocus datasets (Brandley et al. 2011). We ran two independent analyses for 25 million generations sampling every 10,000 generations using a birth–death prior on speciation, and examined plots of  $-\ln L$  values in Tracer (Rambaut and Drummond 2007) to ensure convergence of

the two runs. We discarded the first 2.5 million generations in each run as burnin after visually assessing stationarity and ensuring convergence of the two runs on similar optima, and combined the log and tree files for a total of 45 million postburnin generations. Convergence was assumed when the estimated sample size (ESS) for most parameters reached 200 (Drummond et al. 2006). To estimate branch lengths in units of absolute time (millions of years, Ma), we applied the following temporal and topological constraints to five nodes, based on the fossil record:

- (1) *Root node*: Normal distribution, mean = 169.5 Ma, SD = 12.5, 95% prior credible interval (PCI) = 145–194 Ma. The nearest outgroup to the snakes is unclear, but most evidence suggests Anguimorpha, Iguania, or a clade containing both of those groups (Vidal et al. 2009; Vitt and Caldwell 2009; Wiens et al. 2010); we used Varanidae. Confidence intervals for the node representing the Most Recent Common Ancestor (MRCA) of Serpentes, Iguania, and Anguimorpha have ranged from 145 to 194 Ma, with most studies inferring a date between 158 and 178 Ma (Vidal et al. 2009). Thus, we place a normally distributed prior on this node.
- (2) *MRCA of Alethinophidia*: Normal distribution, mean = 102.75 Ma, 95% PCI = 93.5–112.0 Ma. Recent phylogenetic analyses strongly support the placement of several “snakes with legs” and relatives (*Haasiophis*, *Pachyrhachis*, and *Eupodophis*) in the crown-group Alethinophidia (Tchernov et al. 2000; Wiens et al. 2010), indicating a minimum age of 93.5 Ma for this node from the ages of those fossil species. The oldest known snake fossils from the Aptian–Albian boundary (Rage 1984; Rage 1987) provide a rough older bound on the age of this node approximately 112.0 Ma (Vidal et al. 2009).
- (3) *Stem-group age of Colubroidea*: minimum of 48.6 Ma. Based on the Eocene (Ypresian: 55.8–48.6 Ma) snake *Procerophis*, the oldest known colubroid (Rage et al. 2008), we place a minimum of 48.6 Ma on the divergence between Acrochordidae and Colubroidea. We place a maximum of 112.0 Ma on this node, consistent with the constraints on the MRCA of Alethinophidia, using a uniform distribution. We use a uniform distribution for this node, as a more informative prior (e.g., a lognormal distribution) would not be based on robust fossil data, as information for the parameters (i.e., the mean and variance) is not given by the fossil record.
- (4) *Stem-group age of Colubridae*: minimum of 33.3 Ma. Based on the Oligocene (Orellan: 33.9–33.3 Ma) snake *Texasophis galbreathi*, the oldest known colubrid (Holman 2000), we place a minimum of 33.3 Ma on the divergence between Elapidae, Lamprophiidae, and Colubridae, and a maximum of 112.0 Ma, consistent with the constraints on the MRCA of Alethinophidia, using a uniform distribution. As with the

previous constraint, robust information for parameterizing a more informative prior is not available in the fossil record, as the minimum comes from the oldest known fossil, and medians or older limits are thus unknown.

### PHYLOGENETIC DIVERSIFICATION ANALYSES

We used the MEDUSA algorithm (Alfaro et al. 2009) to determine if extant snake diversity could be explained by background rates of speciation and extinction, or whether significant increases or decreases in the rate of diversification were present in the major lineages. Using the Reptile Database (Uetz 2009), we classified 3256 species of snake (>99% of the known extant diversity) into each of the 40 terminal lineages in our tree, including several recent revisions to snake taxonomy (Appendix S1). Given the dated chronogram from the BEAST analysis and the number of species in each terminal family or subfamily, we tested for significant variation in diversification rates throughout the history of the extant snakes. The MEDUSA algorithm fits a single-rate model to the entire tree, then fits a series of increasingly complex (e.g., 2-rate, 3-rate, etc.) models, with rate shifts occurring at the internal branches giving the highest likelihood (sensu Rabosky et al. 2007). These models are then compared using corrected Akaike information criterion (AICc) to choose the best-fit model. We used the runMedusa and summaryMedusa commands in the R package GEIGER (Harmon et al. 2008), and chose the model with the lowest AICc value.

When fitting models to data, it is still possible that the best-fit model is still a relatively poor one. Thus, to assess the fit of the best-fit MEDUSA and other models (see below), we performed posterior predictive simulations to determine how well data simulated under the chosen models matched the observed data. We simulated 5000 sets of clade sizes based on the MEDUSA results, drawing clade sizes from a geometric distribution given the parameters for each rate shift. We compared these to the observed data using three summary metrics (Rabosky 2010a), standard deviation (SD) of clade size, logarithm of maximum clade size (LN), and the Spearman’s correlation coefficient between age and diversity (ADC). This allows us to quantify the match between the best-fit models and the data, based on several crucial summary statistics.

### CLADE-BASED DIVERSIFICATION ANALYSES

First, we identified clades with both more and fewer species than expected given background diversification rates (Magallón and Sanderson 2001) by calculating the 95% confidence limits on clades size given the stem-group age, diversification rate, and extinction fraction. These are implemented in the lambda.stem.ci command in the R package LASER (Rabosky 2006). We used the net diversification rate (0.031) and extinction fraction (0.62) from the background (whole-tree) diversification model calculated in MEDUSA, which takes data on the total diversity of extant

lineages into account. We also calculated confidence limits under an arbitrarily high (0.90) extinction fraction (Magallón and Sanderson 2001). If the standing diversity of snakes is explained by simple birth–death processes under background rates of speciation and extinction, then we would expect to see the majority of lineages fall within the 95% confidence limits on clade size implied by these models. Note, however, that other, more complex models (such as the multiple-rate birth–death models calculated in MEDUSA as well as others) may also yield a similar distribution of clade ages and sizes.

Second, we tested for a relationship between clade age and diversity in terminal lineages to determine if the time-for-speciation effect explains diversity patterns in clades (see Stephens and Wiens 2003; McPeck and Brown 2007). The lack of a relationship might suggest large-scale variation in diversification rate, correlated speciation–extinction dynamics, or the presence of ecological limits on clade size and long-term faunal turnover at equilibrium (Rabosky 2009a,b). For the extant lineages, we calculated diversification rates using the stem-group method-of-moments estimator of Magallón and Sanderson (2001, eq. 6), with the extinction fraction from MEDUSA (0.62). We used Spearman’s rank correlation to determine if extant diversity in clades is related to diversification rate, and if diversification rate is related to clade age.

To determine if our division of the tree into higher taxa was influencing the relationship between age and diversity, we randomly resampled the tree such that the extant groups were collapsed into higher level taxa, for which the age–diversity relationship was recalculated. This was repeated 100 times for datasets of 11 nodes (approximately 25% of the total nodes), so that the empirical age–diversity correlation could be compared to the randomized distribution. As these points are not phylogenetically independent, we also tested these correlations using phylogenetically independent contrasts (Felsenstein 1985) using the “pic” function in the R package APE (Paradis et al. 2004) using the Bayesian inference (BI) branch lengths. Although this is not an optimal solution, it is unclear how to fully account for the nonindependence of these datapoints.

Finally, we tested whether the distribution of extant clade ages and sizes was better described by (1) a rate-limited model, in which clade age and diversification rate determine clade size (Nee et al. 1994), (2) a model in which net diversification has gone to zero over time and clade size is determined by ecological limits yielding set amounts of time-integrated speciation ( $\Omega$ ), approximated by the logarithm of diversity (Rabosky 2010a), or (3) an extinction-limited model, in which clades undergo an initial birth–death diversification up to the “hL” of clades, and afterwards transition to a “death–birth” model, with deterministic extinction, negative net diversification, and relative extinction fractions greater than 1 (Appendix). We define the hL of clades

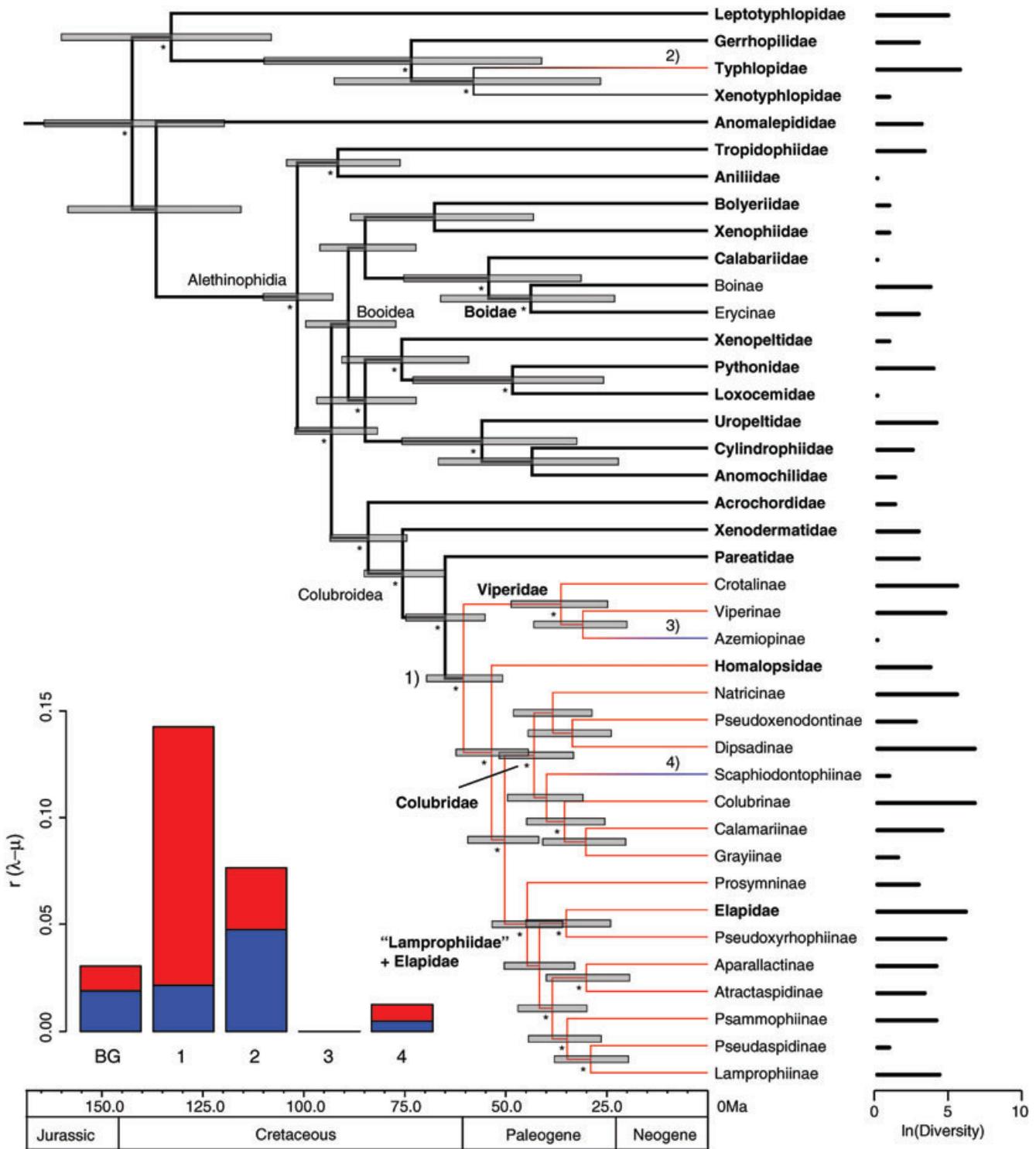
as the time that maximizes the age–diversity correlation of the initial birth–death period (see Appendix). We tested the relaxed forms of the first two models, in which each clade has its own rate or  $\Omega$ , drawn from a gamma distribution, and the constant-parameter form of all models, in which all clades have the same rates, extinction fractions, half lives, or  $\Omega$ . To compare model fit, we simulated 5000 sets of clade sizes drawn from a geometric distribution given the estimated parameters from the models. We compared this to the observed data using the same three metrics described above: SD, LN, and ADC. Model fitting, simulations, and correlations were performed in R using code newly developed by R. A. P. or supplied by D. L. Rabosky.

## Results

### PHYLOGENY AND DIVERGENCE TIMES

The phylogenetic relationships estimated from the 29-gene dataset (Fig. 2) are highly congruent with previous analyses of various subsets (Vidal and Hedges 2002; Lawson et al. 2004; Gower et al. 2005; Vidal et al. 2007, 2009, 2010; Wiens et al. 2008), representing the first phylogeny to include all known snake families and subfamilies based on molecular data. In concordance with previous studies, we find a sister relationship between the enigmatic Xenophiidae and Bolyeriidae (Lawson et al. 2004), and between the poorly known Anomochilidae and Cylindrophiiidae (Gower et al. 2005). As with previous studies, monophyly of Booidea is weakly supported (Noonan and Chippindale 2006; Burbrink and Pyron 2008; Wiens et al. 2008). Another continually problematic clade is the primarily African family Lamprophiidae, which is often found to be paraphyletic with respect to Elapidae, or weakly supported as monophyletic (Vidal et al. 2008; Kelly et al. 2009; Pyron et al. 2011). Here, we find that Lamprophiidae is paraphyletic with respect to Elapidae, with strong support for a sister relationship between Elapidae and the Malagasy subfamily Pseudorhophiinae, and weak support for the placement of this clade with respect to the rest of “Lamprophiidae” (Fig. 2). Although we continue to recognize “Lamprophiidae” and Elapidae (Pyron et al. 2011), we note that this group is a priority for future phylogenetic investigation.

Divergence-time estimates are also highly concordant with previously reported ages (Noonan and Chippindale 2006; Burbrink and Pyron 2008; Vidal et al. 2009, 2010). Crown-group snakes arose around the Jurassic–Cretaceous boundary, 140.8 Ma (95% highest posterior density [HPD] = 120.7–161.4 Ma). Alethinophidia evolved during the mid-Cretaceous, 101.5 Ma (95% HPD = 93.1–109.8 Ma), whereas Booidea and Colubroidea both originated in the late Cretaceous, 90.0 Ma (95% HPD = 79.1–100.0 Ma) and 84.7 Ma (95% HPD = 76.0–93.4 Ma), respectively. These estimates are concordant with previous molecular divergence-time estimates



**Figure 2.** Phylogeny of the extant snakes, containing all families and subfamilies, based on a concatenated dataset of up to 29 genes (18,924 bp) per species. The tree represents 45 million postburnin generations, estimated in the program BEASTv1.6.1. Numbers on branches correspond to the graph comparing background (BG) rates of diversification to the four significant rate shifts. The blue bars represent the extinction fraction (turnover rate). Nodes supported with  $P > 0.95$  are indicated with an asterisk (\*), and bars represent 95% HPDs for mean date estimates. Lineage diversity is indicated at right, on a log scale.

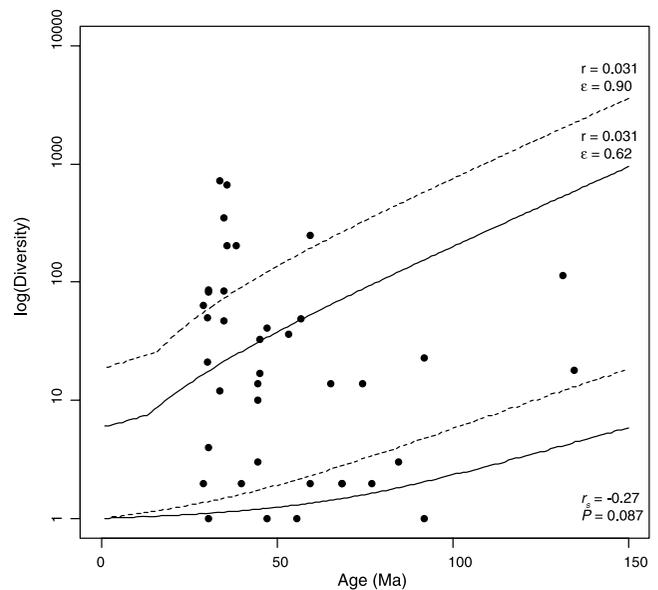
(e.g., Burbrink and Pyron 2008; Vidal et al. 2009), and consistent with other paleontological data not included in the analyses that suggest snakes arose in the Jurassic or Cretaceous, and diversified primarily in the Cenozoic (Rage 1984, 1987; Holman 2000; Vidal et al. 2009; Vitt and Caldwell 2009).

### DIVERSIFICATION ANALYSES

The MEDUSA analysis identifies a birth–death model (background  $r_0 = 0.031$  and  $\epsilon_0 = 0.62$ ) with four diversification rate shifts, two increases and two decreases, as the best-fit model accounting for the extant diversity of snakes (Fig. 2). The blindsnake family Typhlopidae exhibits a 2.5-fold increase in diversification rate ( $r_1 = 0.077$ ,  $\epsilon_1 = 0.62$ ). Also, we find a 4.6-fold increase at the node subtending the colubroid families Viperidae, Homalopsidae, Elapidae, Lamprophiidae, and Colubridae ( $r_2 = 0.143$ ,  $\epsilon_2 = 0.15$ ), including most colubroid species (Fig. 2). Within this clade, rates decreased significantly in the subfamilies Azemiopinae ( $r_3 = 2.27 \times 10^{-17}$ ,  $\epsilon_3 = 3.9 \times 10^{-6}$ ) and Scaphiodontophiinae ( $r_4 = 0.012$ ,  $\epsilon_4 = 0.37$ ). Note that some authors have suggested that this last clade is allied with *Sibynophis* based on morphological data (Zaher 1999), thus increasing the number of species to approximately 11 (thus potentially not representing a significant rate decrease) and giving it the name Sibynophiinae, but we await publication of molecular data bearing on this issue before making any alterations (Burbrink et al., unpubl. ms.).

Clade age and rate estimates from MEDUSA are significantly negatively correlated ( $r_s = -0.64$ ,  $P < 0.00001$ ), indicating that older clades have lower estimated rates. The MEDUSA model does not provide unambiguous support for rate increases restricted to any of the lineages composed solely of venomous species, or any of the lineages endemic to the NW. However, the rate shift in Colubroidea (“1”; Fig. 2) subtends all venomous snakes, including medically significant species in the families Homalopsidae and Colubridae, and several exceptionally diverse NW groups. Although these potential sources of ecological opportunity are insufficient alone to explain species richness in colubroids, both may have contributed to the exceptional diversity of the group through various mechanisms (see below).

Using both the estimated ( $\epsilon_0 = 0.62$ ) and high ( $\epsilon = 0.90$ ) extinction fractions and the maximum-likelihood (ML) diversification rate of 0.031 lineages per million years, at least 10 and as many as 16 lineages have more species than expected, and at least four and as many as nine lineages have fewer (Fig. 3; Table 1). In contrast to expectations under a birth–death model, there is a negative but nonsignificant relationship between clade age and diversity at the subfamily level ( $r_s = -0.27$ ,  $P = 0.087$ ; Fig. 3). Results are similar when phylogenetic nonindependence is partially accounted for using phylogenetically independent contrasts and the BI branch lengths ( $r_s = -0.13$ ,  $P = 0.41$ ). Standing diversity is positively correlated with diver-



**Figure 3.** Plot of clade age against known diversity. There is a negative but nonsignificant relationship between lineage age and species richness ( $r_s = -0.27$ ,  $P = 0.087$ ). The solid lines represent 95% confidence intervals on clade size given background rates of diversification ( $r = 0.031$ ) and turnover ( $\epsilon = 0.62$ ), whereas the dotted lines are the intervals under arbitrarily high extinction ( $\epsilon = 0.90$ ). Lineages with exceptionally high or low diversity are highlighted in Table 1.

sification rate ( $r_s = 0.93$ ,  $P < 0.00001$ ), and diversification rate is negatively correlated with clade age ( $r_s = -0.52$ ,  $P < 0.001$ ). Resampling nodes randomly from the tree results in an average log SD (6.65; range = 6.52–6.68) and log max diversity (7.87; range = 7.75–7.90) of clades higher than that observed in the empirical data (5.1 and 6.6, respectively), and a mean age–diversity correlation of 0.21, with a range from  $-0.22$  to 0.61 (empirical value =  $-0.27$ ). Therefore, both maximum diversity and the correlation between age and diversity differ between the actual named groups used here and the random resampling of clades from the phylogeny. This indicates that the current organization of higher snakes is nonrandom, and thus may represent significant units of study for diversity analyses (see below).

For the clade-based models, a relaxed- $\Omega$  model (diversity-limited), in which species richness of clades is determined by a limit drawn from a gamma distribution, is strongly supported over rate-limited models with variable or constant rates, and a constant- $\Omega$  model (Table 2; Fig. 4). This indicates that variation in clade age and diversification rate alone is likely insufficient to explain the total variation in standing snake diversity. The empirically calculated hL for the extinction-limited model (the age yielding the strongest age–diversity relationship for the extant snakes) is 39 Ma (Fig. 5; see Appendix). With this value, the extinction-limited model is better supported than the constant-rate

**Table 1.** Known families and subfamilies of snakes, and total assigned species (#). Clades with significantly more or fewer species than expected under estimated ( $\epsilon = 0.62$ ; \*, ††) and high ( $\epsilon = 0.90$ ; \*\*, ‡) extinction are noted (Sig.).

Taxon	#	Age	Sig.	Distribution
Acrochordidae	3	84.66	†	TA, OA
Aniliidae	1	91.80	††	NT
Anomalepididae	18	134.59	–	NT
Anomochilidae	3	44.45	–	TA
Aparallactinae	50	30.29	*	AF, PA
Atractaspidinae	21	30.29	*	AF, PA
Azemiopinae	1	30.39	††	TA, PA
Boinae	33	45.02	–	NT, MG, OA, TA
Bolyeriidae	2	68.40	†	MG
Calabariidae	1	55.65	††	AF
Calamariinae	82	30.42	**	TA, OA
Colubrinae	660	35.63	**	NA, NT, PA, TA, AF, OA
Crotalinae	202	35.66	**	NA, NT, PA, TA
Cylindrophiiidae	10	44.45	–	TA, OA
Dipsadinae	722	33.65	**	NA, NT
Elapidae	349	34.86	**	NA, NT, PA, AF, TA, OA
Erycinae	17	45.02	–	NA, NT, PA, AF, TA
Gerrhopilidae	14	74.37	–	TA, OA
Grayiinae	4	30.42	–	AF
Homalopsidae	36	53.38	–	PA, TA, OA
Lamprophiinae	64	28.90	**	AF
Leptotyphlopidae	113	131.27	–	NA, NT, PA, AF, TA
Loxocemidae	1	47.12	††	NT
Natricinae	205	38.28	**	NA, NT, OA, TA, PA, AF
Pareatidae	14	65.39	–	PA, TA
Prosymninae	14	44.51	–	AF
Psammophiinae	47	34.87	*	PA, AF, TA
Pseudaspidae	2	28.90	–	AF
Pseudoxenodontinae	12	33.65	–	PA, TA
Pseudoxyrhophiinae	84	34.86	**	MG, AF
Pythonidae	41	47.12	*	AF, TA, OA
Scaphiodontophiinae	2	39.71	–	NT
Tropidophiidae	23	91.80	–	NT
Typhlopidae	247	59.41	**	NT, PA, AF, TA, OA
Uropeltidae	49	56.84	*	TA
Viperinae	86	30.39	**	PA, AF, TA
Xenodermatidae	17	76.08	–	TA
Xenopeltidae	2	77.00	†	TA
Xenophiidae	2	68.40	†	TA
Xenotyphlopidae	2	59.41	†	MG

Distribution: TA = Tropical Asia, NT = Neotropics, AF = Tropical Africa, MG = Madagascar, PA = Palearctic, OA = Oceania, NA = Nearctic.

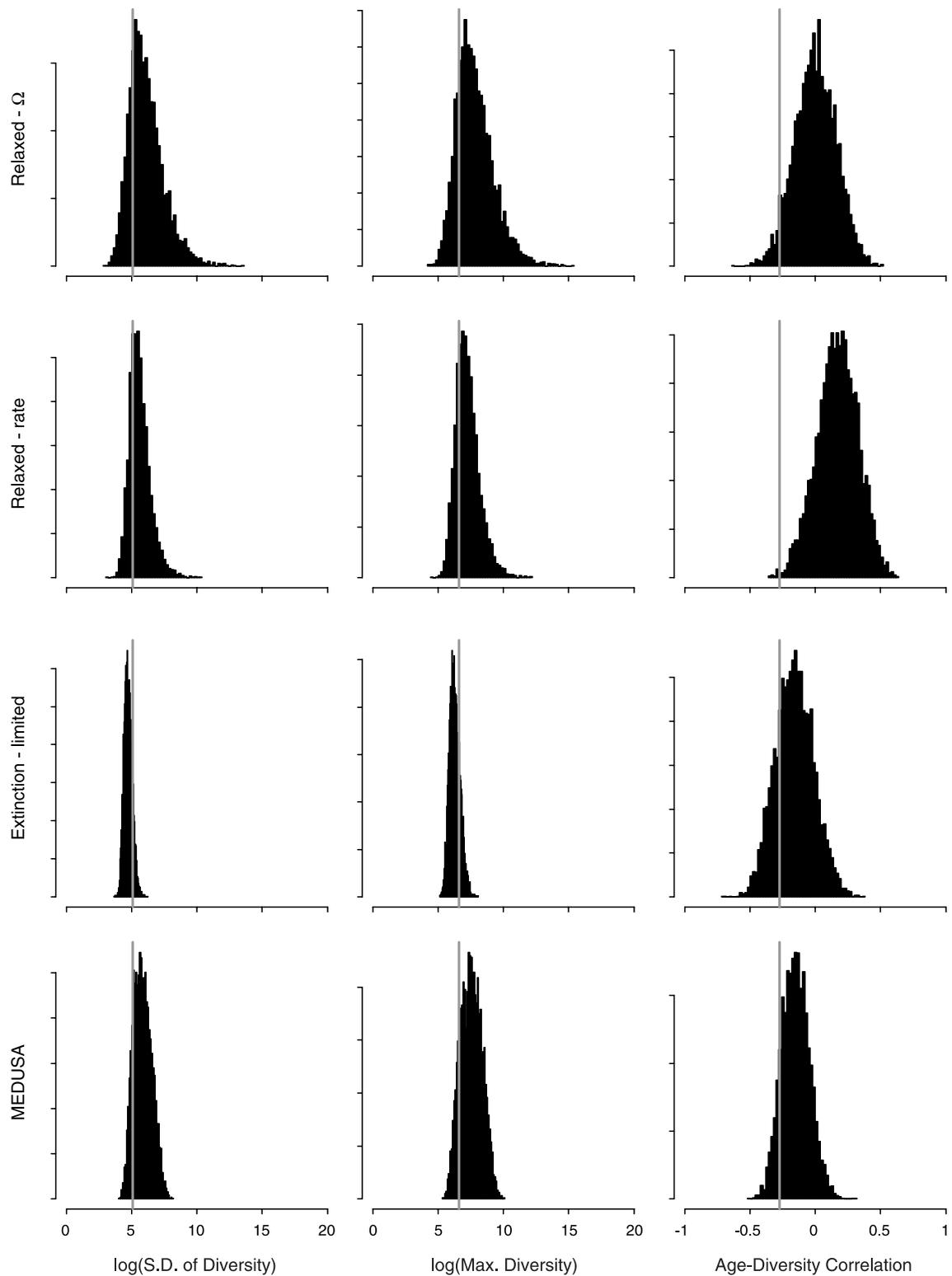
model, but less so than the relaxed forms of those models, or the diversity-limited models (Table 2). The estimated rate for the initial increase (0.15) yields an expected clade size of approximately 350 species after initial diversification. Clade diversities simulated under the rate-limited, diversity-limited, and MEDUSA models all produce results consistent to some degree with the variance and maximum size of the observed snake lineages, although none can adequately account for the negative correlation between clade age and diversity (Fig. 4). In contrast, data simulated under the extinction-limited model provide a much closer fit to the observed data (Fig. 4).

## Discussion

### PATTERNS OF GLOBAL SNAKE DIVERSITY

Standing diversity in snakes varies by at least two orders of magnitude among subfamilies (Table 1), with many clades containing many more or fewer species than would be expected given background rates of speciation and extinction (Figs. 2, 3). However, this diversity is not related to stem-group age, and numerous ancient lineages are represented by only one or two species (Figs. 2–3). Curiously, the most diverse snake lineages and the ancient, species-poor clades all inhabit tropical regions of the world (Table 1). Thus, explanations relying on the gradual accumulation of lineages over time to explain diversity within lineages or areas (e.g., Stephens and Wiens 2003; Wiens and Donoghue 2004; McPeck and Brown 2007; Pyron and Burbrink 2009) do not appear sufficient to explain global diversity patterns in extant snakes. It can be extremely difficult to separate speciation and extinction rates given only a molecular phylogeny (Ricklefs 2007; Rabosky 2009a), and even more difficult to uncover potential mechanisms for their variation. However, preliminary hypotheses can be offered for two primary drivers of diversification: (1) the evolution of venom delivery and (2) colonization of new areas.

The MEDUSA algorithm indicates significant rate increases within the superfamily Colubroidea, at the node subtending all venomous species and the majority of nonvenomous species, which exhibits a putative 4.5-fold increase in net diversification rate (Fig. 2). This provides potential support for the impact of advanced venom-delivery systems as a key innovation for diversification. Many dangerously venomous species are known in several of these putatively “nonvenomous” clades (e.g., boomslangs and twigsnakes in Colubrinae; Greene 1997), and potentially a large number of other colubroids (Fry et al. 2003, 2006). Thus, the presence of toxic salivary components, at a level that is subclinical for humans (see Fry et al. 2008), may have nonetheless enabled colubroid snakes to undergo exceptional diversification by conferring an advantage for prey capture, increasing the breadth of potential prey, and thus increasing



**Figure 4.** Results of 5000 posterior simulations to evaluate accuracy of three diversification models fit to the data on extant snake diversity (Table 2) and the MEDUSA algorithm. The parameters evaluated are the natural logarithm of the standard deviation of species richness, the natural logarithm of maximum clade size, and the Spearman's rank correlation between clade age and diversity. Observed values are indicated with gray lines.

**Table 2.** Likelihoods of different diversification models applied to the extant snake lineages, accounting for rate-limited and extinction-limited dynamics and ecological limits on diversity.

Model	$-\ln L$	#P	AIC	Estimates
Relaxed- $\Omega$	-196.16	2	396.33	$\alpha=4.22$ ; $\beta=1.25$
Relaxed-rate	-197.04	3	400.08	$\alpha=0.45$ ; $\beta=147.88$ , $\varepsilon=0.999$
Constant- $\Omega$	-215.73	1	433.46	$\Omega=4.40$
Constant $\varepsilon$ -limited	-216.59	4	441.17	$r_0=0.15$ , $\varepsilon_0=0$ , $r_1=-0.39$ , $\varepsilon_1=1.014$
Constant-rate	-225.44	2	454.88	$r=0$ , $\varepsilon=1.0$
MEDUSA (4-rate)	-320.29	14	668.58	$r_0=0.031$ , $\varepsilon_0=0.62$

Note that the MEDUSA model was chosen using AICc (675.14), and is based on combined phylogenetic–taxonomic data, compared to purely taxonomic estimators for the other models (see Rabosky et al. 2007). See text and Figure 2 for estimated rate shifts from MEDUSA. For the parameters,  $\alpha$  and  $\beta$  are the shape and scale of the gamma distribution of clade size ( $\Omega$ ), whereas  $r$ ,  $r_0$ , and  $r_1$  are estimates of diversification rate, and  $\varepsilon$ ,  $\varepsilon_0$ , and  $\varepsilon_1$  are estimates of the extinction fraction, under either the constant ( $r$ ,  $\varepsilon$ ) or time-variable ( $r_0$ ,  $\varepsilon_0$ ;  $r_1$ ,  $\varepsilon_1$ ) models.

speciation rates. This is a hypothesis in need of further study, given the prevalence and diversity of salivary toxins in an apparent majority of colubroid snake species (Fry et al. 2003, 2008) and potentially a large proportion of extant squamates (Fry et al. 2006).

The ecological opportunity encountered after colonizing the NW also does not appear to be the sole driver of colubroid diversification, despite over a third of all snake species (Vitt and Caldwell 2009) having originated there since the Oligocene (Fig. 2, Table 1). However, dispersal into the NW has represented a significant source of ecological opportunity for some lineages (Burbrink and Pyron 2010), and resulted in massive diversification and adaptive radiation in the Neotropics (Cadle and Greene 1993). However, colubroids likely originated in the Old World (OW) tropics and are particularly diverse there as well, despite co-occurring with up to 20 other lineages representing potential competitors (Head et al. 2005; Vitt and Caldwell 2009). Thus, the ecological opportunity presented by dispersal into the NW appears insufficient alone to explain the total diversity of colubroids, although a significant contribution is likely, given patterns observed in some lineages (e.g., Cadle and Greene 1993; Burbrink and Pyron 2010). The colonization of novel habitats and areas free of competitors is a well-known trigger for exceptional radiation through elevated speciation in a variety of regions and organisms (Losos and Schluter 2000; Yoder et al. 2010).

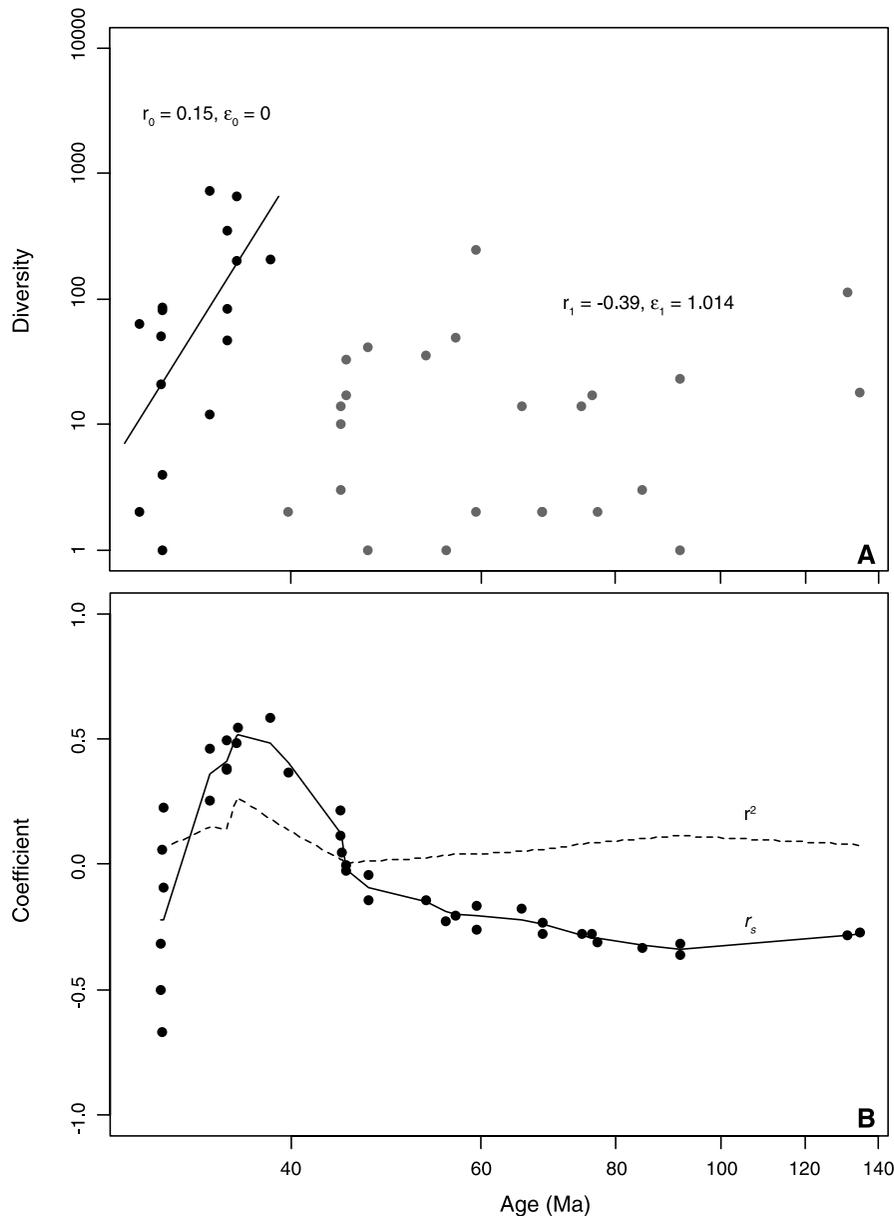
#### MODELING DIVERSIFICATION THROUGH TIME

If our rate estimates are accurate, the negative relationships between clade age, diversity, and estimated diversification rate provides a clear explanation for observed patterns, with older clades having fewer species due to their lower rates. However, the lack of support for rate-limited models suggests that these relationships are artifactual. If rates decay across time within lineages, then older clades should still have relatively high diversity, stemming from an early period of higher diversification, because all old lin-

ages were once young and would have had higher rates. Thus, this explanation requires that older groups have always exhibited low rates, implying that clades originating earlier in the history of snakes have intrinsically lower diversification rates up to than 17 orders of magnitude (Fig. 2). This would seem to make little sense, implying that the ability to diversify is a recent innovation, which is contradicted by the fossil record of the group (see Rage 1984, 1987).

In contrast, a diversity-regulated model fits the observed data better than rate-limited models (although only slightly =  $\Delta AIC = 3.75$ ; Table 2). Thus, results from analyses such as MEDUSA may simply reflect differences in total speciation. However, this model makes two assumptions that may not be warranted: that the standing diversity of snakes has been maintained at current levels through time, and that clades do not vary through time in either rates of speciation and extinction, or maximum clade size. For example, lineages such as Aniliidae, medium-sized (approximately 0.75 m) burrowing snakes from South America, are currently represented by a single species. It seems unlikely that Aniliidae is currently limited to a single species by ecological factors. Although aniliids were far more diverse in the past (Rage 1984), it also seems equally unlikely that they attained diversities in the hundreds of species, comparable to those seen in South American dipsadine assemblages (Cadle and Greene 1993). Given that all depauperate lineages exist in areas renowned for their exceptional diversity of snakes and other organisms (e.g., the Amazon Basin, Madagascar), it is unclear what ecological mechanism could explain their limitation compared to the other snake lineages.

Here, we find that the extinction-limited model provides a better fit to the data than constant-rate models, and only slightly worse than diversity-limited models (Table 2). Numerous snake lineages were more diverse in the past as evidenced in the fossil record (Rage 1984, 1987; Holman 2000), and have either gone extinct (e.g., Anomalopneidae, Lapparentophiidae, Dinilysiidae,



**Figure 5.** Illustration of patterns from extinction-limited model for the snakes, showing the age–diversity relationship on a log–log scale, with the initial positive age–diversity relationship and secondary loss of that signal, and the rate ( $r_0$  and  $r_1$ ) and extinction fractions ( $\varepsilon_0$  and  $\varepsilon_1$ ) for the two time periods (A), and the Spearman correlation coefficient and  $r^2$  through time for the age–diversity relationship (B). The regression lines (A) show the difference between the two stages, and lowest smoothed curves (period = 1/5) show the change in  $r_s$  and  $r^2$  through time (B).

Madtsoiidae, Nigerophiidae, Pachyophiidae, Palaeophiidae, Russellophiidae, etc.), or undergone significant reductions in diversity (e.g., Aniliidae, Boidae) not accounted for by rate- or diversity-limited models. The extinction-limited model also predicts a more realistic distribution of maxima and variation in species richness and the age–diversity correlation compared to the other models in simulation, particularly birth–death models (Fig. 4; Table 2). Incorporating deterministic extinction can explain the lack of extremely diverse old groups and the prevalence of depauperate old

clades, while explaining the positive age–diversity correlation in young clades (Figs. 1–5). Future implementations will feature a relaxed version, and previous studies suggest that such a model, in which clades have variable rates and “half lives,” may fit substantially better, as seen in relaxed-rate and relaxed- $\Omega$  models (Rabosky 2010a).

The generality of the extinction-limited model requires further study to evaluate the prevalence of negative or hump-shaped age–diversity relationships. Also, note that our data, as with

most studies, only account for stem-group ages (see Rabosky 2009b). Without a more fully sampled phylogeny, it is impossible to determine crown-group ages for all clades. However, although some would clearly be younger (e.g., Acrochordidae: stem age of approximately 85 Ma vs. crown age of approximately 16–20 Ma; Sanders et al. 2010), monotypic lineages would remain unchanged, and many (e.g., scolecophidians; Vidal et al. 2010) would appear to vary little (although estimating crown-group ages requires that all basal lineage be included). If crown-group ages are positively correlated with stem-group ages, their use would presumably make little difference. If they are not, and diversity shows a positive relationship with crown ages, but an insignificant or negative relationship with stem ages, this would suggest the initial diversification of clades is rate limited, but that extinction drives the disconnect between stem ages and richness through time.

This approach also makes the assumption, along with rate- and diversity-limited processes, that higher level taxa (clades) are truly meaningful in a biological sense. The delimitation of clades remains a topic of crucial importance, as it may be possible to divide a tree up into in an arbitrary way to produce nearly any pattern. Here, randomly resampling clades yields a narrow distribution of parameter estimates, suggesting that the current division of extant snakes into clades is nonrandom. However, in snakes as in most groups, the definition of higher taxa is either implicitly or explicitly based on notions of biogeographic or ecomorphological cohesiveness (e.g., vipers, elapids, boas, pythons, etc.; Vitt and Caldwell 2009). Thus, dividing the gnathostomes (for instance) into random clades would likely rarely yield such obviously biologically significant groups as salamanders, birds, and placental mammals. Whether these divisions are comparable among lineages, and the degree to which these definitions are based on quantitative analyses, should be an important consideration of future analyses.

#### CLADE-LEVEL EXTINCTION AND DIVERSITY PATTERNS

Recent literature has contrasted two alternative models of diversification, one in which speciation is rate limited and continues unbounded through time, and one in which clade size is diversity regulated, with upper limits on species richness that are decoupled from clade age (Stephens and Wiens 2003; Ricklefs 2006, 2007; McPeck and Brown 2007; Rabosky 2009a,b, 2010a). Here, the greatest support is obtained for diversity-limited models when considering both numerical fit and posterior simulation. However, although ecological factors such as area and energy are commonly linked to diversity (Rosenzweig 1995), the mechanisms responsible for these relationships are unclear (Losos and Schluter 2000; Evans et al. 2005; Hurlbert and Jetz 2010). It is also unknown how these processes would act to limit the total number of species

in an ecosystem the way the number of individuals is limited in a population. These models also predict biologically unreasonable distributions of clade size, up to  $e^{10}$  or  $e^{15}$  at recent time scales (Fig. 4; Rabosky 2010a), further suggesting that they may be flawed for modeling diversity across long periods of time. Additionally, there are numerous cases of negative age–diversity relationships (Rabosky 2009b), which are not easily explained by either process. This might be an indication that neither address processes associated with declining diversity or deterministic extinction, thus skewing predictions for extant species richness. Although both rate- and diversity-limited models allow for stochastic events, as all clades may have a nonzero probability of extinction, neither allows the relative extinction fraction ( $\epsilon$ ) to exceed 1.

All species eventually decline and go extinct (e.g., Foote et al. 2007). We might thus expect most lineages to undergo an initial diversification, and either diverge into new adaptive zones (e.g., Simpson 1953), or eventually decline to extinction due to the failure of species to adapt to continually changing environments over long time scales (van Valen 1973; Futuyma 2010). This would produce a hump-shaped age–diversity relationship (Fig. 1). There is no reason to expect that a given group, such as aniliid snakes or tuataras, will always have organisms best adapted to their environment, and perpetually maintain or increase in diversity, rather than go extinct or diverge into substantially different daughter clades. Thus, this process may arise naturally as new traits arise in different groups adapting to continually changing environments through time, outcompeting existing lineages. The ascendance and senescence of clades is a relatively common pattern in the fossil record (Sloss 1950; Van Valen 1975; Thomson 1976; Gould et al. 1977; Foote 2007; see Strathmann and Slatkin 1983; Raup 1985), including many snake groups (Rage 1987). Examples are known in many other groups, including birds, mammals, and bivalves (Van Valen 1975; Vuilleumier 1984; Flessa and Jablonski 1996).

The peak of diversity and length of ascendance and senescence should thus be linked to the adaptability of the group (Futuyma 2010), the extinction tolerance of species (Waldron 2010), and potentially the maximum diversity of clades set by ecological factors (Rabosky 2010a). However, if diversity is viewed as the outcome of a speciation process countered by the forces of continually changing environments, apparent limitation of clade size can be seen to stem not from ecological limits, but simply the peak richness attained by a given clade before it begins to decline toward extinction. Niche conservatism (Wiens and Graham 2005) therefore provides a simple mechanism for the decline of lineages when environments change along an axis that is strongly conserved, such as thermal tolerance (Sinervo et al. 2010), or pathogen resistance (Pounds et al. 2006). The heritability and adaptability of traits can explain the success of some groups across long periods of time compared to their sister

lineages (such as tuataras and squamates), explaining why all clades have not gone extinct, a previous criticism of extinction-limited models (Rabosky 2010a). At any given time, a number of clades may be ahead of the curve due to colonization of new areas, extinction of competitors, or the evolution of key innovations, and exhibit exceptional diversity (Simpson 1953; Losos 2010; Yoder et al. 2010).

At present, it seems unlikely that purely rate-limited processes can explain patterns in the standing diversity of many groups, whereas diversity-limited processes are of uncertain biological interpretation (Ricklefs 2006, 2007; Rabosky 2009a,b; Wiens 2011). We suggest that many aspects of extant species richness patterns, including vast disparities between sister taxa and insignificant or negative relationships between clade age and diversity, can be explained by the failure of some lineages to respond to continually changing environments over long time scales. Both rate- and diversity-limited models typically assume either implicitly or explicitly that the sum of the interaction between organisms and their environment results in relative extinction fractions ( $\epsilon$ ) bound between 0 and 1. However, the fossil record suggests that many organisms (and as we suggest, groups of related organisms) may ultimately “lose” the evolutionary arms race, with the sum of the organism–environment interaction resulting in  $\epsilon > 1$  (Van Valen 1973, 1975; Jablonski 2008; Rabosky and McCune 2010). Such a process will lead to a hump-shaped distribution of diversity through time, potentially mimicking rate variation and ecological limits. This provides a third alternative model for explaining diversity patterns through time, and merits further study using both paleontological and neontological data.

## ACKNOWLEDGMENTS

We would like to thank H. Alamillo, L. J. Harmon, and M. E. Alfaro for sharing preliminary results and assistance with MEDUSA, D. L. Rabosky for providing R code and discussing many of these issues, and D. B. Shepard, T. J. Guiher, J. M. Clark, and the GWU systematics discussion group for reviewing early drafts of this manuscript, and X. Hua for assistance with models. This research was funded by NSF grant DBI-0905765 awarded to R. A. P.

## LITERATURE CITED

- Alfaro, M. E., F. Santini, C. D. Brock, H. Alamillo, A. Dornburg, D. L. Rabosky, G. Carnevale, and L. J. Harmon. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl. Acad. Sci. USA* 106:13410–13414.
- Bokma, F. 2003. Testing for equal rates of cladogenesis in diverse taxa. *Evolution* 57:2469–2474.
- Brandley, M. C., Y. Wang, X. Guo, A. Nieto Montes de Oca, M. Fería Ortíz, T. Hikida, and H. Ota. 2011. Accommodating heterogeneous rates of evolution in molecular divergence dating methods: an example using intercontinental dispersal of *Plestiodon* (*Eumeces*) lizards. *Syst. Biol.* 60:3–15.
- Burbrink, F. T., and R. A. Pyron. 2008. The taming of the skew: estimating proper confidence intervals for divergence dates. *Syst. Biol.* 57:317–328.
- . 2010. How does ecological opportunity influence rates of speciation, extinction, and morphological diversification in New World ratsnakes (tribe Lampropeltini)? *Evolution* 64:934–943.
- Burbrink, F. T., and B. I. Crother. 2011. Evolution and taxonomy of snakes. Pp. 19–53 in R. A. Aldridge and D. M. Sever, eds. *Reproductive biology and phylogeny of snakes*. Science Publishers, Enfield, NH.
- Butlin, R., J. Bridle, and D. Schluter. 2009. *Speciation and patterns of diversity*. Cambridge Univ. Press, Cambridge.
- Cadle, J. E., and H. W. Greene. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. Pp. 281–293 in R. E. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities: historical and geographical perspectives*. Univ. of Chicago Press, Chicago.
- Campbell, V., and F. J. Lapointe. 2009. The use and validity of composite taxa in phylogenetic analysis. *Syst. Biol.* 58:560–572.
- . 2010. Retrieving a mitogenomic mammal tree using composite taxa. *Mol. Phylogenet. Evol.* 58:149–156.
- Cardillo, M., C. D. L. Orme, and I. P. F. Owens. 2005. Testing for latitudinal bias in rates of species diversification: an example using New World birds. *Ecology* 86:2278–2287.
- Drummond, A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biol.* 4:699–710.
- Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* 7:214.
- Evans, K. L., P. H. Warren, and K. J. Gaston. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.* 80:1–25.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Fischer, A. G. 1960. Latitudinal variations in organic diversity. *Evolution* 14:64–81.
- Flessa, K. W., and D. Jablonski. 1996. The geography of evolutionary turnover: a global analysis of extant bivalves. Pp. 376–397 in D. Jablonski, D. H. Erwin and J. H. Lipps, eds. *Evolutionary paleobiology*. Univ. of Chicago Press, Chicago.
- Foote, M. 2007. Symmetric waxing and waning of invertebrate genera. *Paleobiology* 33:517–529.
- Foote, M., J. S. Crampton, A. G. Beu, B. A. Marshall, R. A. Cooper, P. A. Maxwell, and I. Matcham. 2007. Rise and fall of species occupancy in Cenozoic fossil mollusks. *Science* 318:1131–1134.
- Foote, M., J. P. Hunter, C. M. Janis, and J. J. Sepkoski, Jr. 1999. Evolutionary and preservational constraints on origins of biologic groups: divergence times of eutherian mammals. *Science* 283:1310–1314.
- Fry, B. G., W. Wüster, S. F. R. Ramjan, T. Jackson, P. Martelli, and R. M. Kini. 2003. LC/MS/MS (liquid chromatography, mass spectrometry) analysis of Colubroidea snake venoms: evolutionary and toxicological implications. *Rapid Commun. Mass Spectrom.* 17:2047–2062.
- Fry, B. G., N. Vidal, J. A. Norman, F. J. Vonk, H. Scheib, S. F. R. Ramjan, S. Kuruppu, K. Fung, S. B. Hedges, M. K. Richardson, et al. 2006. Early evolution of the venom system in lizards and snakes. *Nature* 439:584–588.
- Fry, B. G., H. Scheib, L. van der Weerd, B. Young, J. McNaughtan, S. F. R. Ramjan, N. Vidal, R. E. Poelmann, and J. A. Norman. 2008. Evolution of an arsenal. *Mol. Cell Proteomics* 7:215–246.
- Futuyma, D. J. 2010. Evolutionary constraint and ecological consequences. *Evolution* 64:1865–1884.
- Gamble, T., A. M. Bauer, G. R. Colli, E. Greenbaum, T. R. Jackman, L. J. Vitt, and A. M. Simons. 2011. Coming to America: multiple origins of New World geckos. *J. Evol. Biol.* 24:231–244.

- Gould, S. J., D. M. Raup, J. J. Sepkoski, T. J. M. Schopf, and D. S. Simberloff. 1977. The shape of evolution: a comparison of real and random clades. *Paleobiology* 3:23–40.
- Gower, D. J., N. Vidal, J. N. Spinks, and C. J. McCarthy. 2005. The phylogenetic position of Anomochilidae (Reptilia: Serpentes): first evidence from DNA sequences. *J. Zool. Syst. Evol. Res.* 43:315–320.
- Greene, H. W. 1997. Snakes: the evolution of mystery in nature. Univ. of California Press, Berkeley, CA.
- Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24:129–131.
- Head, J. J., P. A. Holroyd, J. H. Hutchison, and R. L. Ciochon. 2005. First report of snakes (Serpentes) from the late middle Eocene Pondaung Formation, Myanmar. *J. Vert. Paleontol.* 25:246–250.
- Holman, J. A. 2000. Fossil snakes of North America: origin, evolution, distribution, paleoecology. Indiana Univ. Press, Bloomington, IN.
- Hurlbert, A. H., and W. Jetz. 2010. More than “More Individuals”: the nonequivalence of area and energy in the scaling of species richness. *Am. Nat.* 176:E50–E65.
- Jablonski, D. 2002. Survival without recovery after mass extinctions. *Proc. Natl. Acad. Sci. USA* 99:8139–8144.
- . 2008. Species selection: theory and data. *Ann. Rev. Ecol. Evol. Syst.* 39:501–524.
- Kelly, C. M. R., N. P. Barker, M. H. Villet, and D. G. Broadley. 2009. Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. *Cladistics* 25:38–63.
- Lawson, R., J. B. Slowinski, and F. T. Burbrink. 2004. A molecular approach to discerning the phylogenetic placement of the enigmatic snake *Xenophidion schaeferi* among the Alethinophidia. *J. Zool.* 263:285–294.
- Levinton, J. S. 1979. A theory of diversity equilibrium and morphological evolution. *Science* 204:335–336.
- Losos, J. B. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am. Nat.* 175:623–639.
- Losos, J. B., and D. Schluter. 2000. Analysis of an evolutionary species-area relationship. *Nature* 408:847–850.
- Magallón, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. *Evolution* 55:1762–1780.
- McPeck, M. A., and J. M. Brown. 2007. Clade age and not diversification rate explains species richness among animal taxa. *Am. Nat.* 169:E97–E106.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, et al. (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* 10:315–331.
- Nee, S., R. M. May, and P. H. Harvey. 1994. The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society of London B* 344:305–311.
- Noonan, B. P., and P. T. Chippindale. 2006. Dispersal and vicariance: the complex evolutionary history of boid snakes. *Mol. Phylogenet. Evol.* 40:347–358.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Posada, D. 2008. jModelTest: phylogenetic model averaging. *Mol. Biol. Evol.* 25:1253–1256.
- Pounds, J. A., M. R. Bustamante, L. A. Coloma, J. A. Consuegra, M. P. L. Fogden, P. N. Foster, E. La Marca, K. L. Masters, A. Merino-Viteri, R. Puschendorf, et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161–167.
- Pyron, R. A., and F. T. Burbrink. 2009. Can the Tropical Conservatism Hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lampropeltini. *Glob. Ecol. Biogeogr.* 18:406–415.
- Pyron, R. A., F. T. Burbrink, G. R. Colli, A. N. Montes de Oca, L. J. Vitt, C. A. Kuczynski, and J. J. Wiens. 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Mol. Phylogenet. Evol.* 58:329–342.
- Rabosky, D. L. 2006. LASER: a Maximum Likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evol. Bioinform.* 2:247–250.
- . 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.
- . 2010a. Primary controls on species richness in higher taxa. *Syst. Biol.* 59:634–645.
- . 2010b. Extinction rates should not be estimated from molecular phylogenies. *Evolution* 64:1816–1824.
- Rabosky, D. L., and A. R. McCune. 2010. Reinventing species selection with molecular phylogenies. *Trends Ecol. Evol.* 25:68–74.
- Rabosky, D. L., S. C. Donnellan, A. L. Talaba, and I. J. Lovette. 2007. Exceptional among-lineage variation in diversification rates during the radiation of Australia’s largest vertebrate clade. *Proc. Roy. Soc. Lond. Ser. B* 274:2915–2923.
- Rage, J.-C. 1984. Serpentes: encyclopedia of paleoherpetology, v. 11. Gustav Fischer Verlag, Stuttgart, Germany.
- . 1987. Fossil history. Pp. 51–76 in R. A. Siegel, J. T. Collins and S. S. Novak, eds. *Snakes: ecology and evolutionary biology*. McMillan, New York.
- Rage, J.-C., A. Folie, R. S. Rana, H. Singh, K. D. Rose, and T. Smith. 2008. A diverse snake fauna from the early Eocene of Vastan Lignite Mine, Gujarat, India. *Acta Palaeontol. Pol.* 53:391–403.
- Rambaut A., and A. J. Drummond. 2007. Tracer v1.4. Available from <http://beast.bio.ed.ac.uk/Tracer>.
- Rannala, B. 2002. Identifiability of parameters in MCMC Bayesian inference of phylogeny. *Syst. Biol.* 51:754–760.
- Raup, D. M. 1985. Mathematical models of cladogenesis. *Paleobiology* 11:42–52.
- Ricklefs, R. E. 2006. Global variation in the diversification rate of passerine birds. *Ecology* 87:2468–2478.
- . 2007. Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* 22:601–610.
- Ricklefs, R. E., J. B. Losos, and T. M. Townsend. 2007. Evolutionary diversification of clades of squamate reptiles. *J. Evol. Biol.* 20:1751–1762.
- Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge Univ. Press, Cambridge.
- Sanders, K. L., Mumpuni, A. Hamidy, J. J. Head, and D. J. Gower. 2010. Phylogeny and divergence times of filesnakes (Acrochordus): inferences from morphology, fossils and three molecular loci. *Mol. Phylogenet. Evol.* 56:857–867.
- Simpson, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York.
- Sinervo, B., F. Mendez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. V.-S. Cruz, R. Lara-Resendiz, N. Martínez-Méndez, M. L. Calderón-Espinosa, R. N. Meza-Lázaro, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328:894–899.
- Sloss, L. L. 1950. Rates of evolution. *Evolution* 24:131–139.
- Stephens, P. R., and J. J. Wiens. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *Am. Nat.* 161:112–128.

Strathmann, R. R., and M. Slatkin. 1983. The improbability of animal phyla with few species. *Paleobiology* 9:97–106.

Tchernov, E., O. Rieppel, H. Zaher, M. J. Polcyn, and L. L. Jacobs. 2000. A fossil snake with limbs. *Science* 287:2010–2012.

Thomson, K. S. 1976. Explanation of large scale extinctions of lower vertebrates. *Nature* 261:578–580.

Uetz, P. 2009. The reptile database. <http://www.reptile-database.org>. Accessed October, 2010.

Van Valen, L. 1973. A new evolutionary law. *Evol. Theory* 1:1–30.

———. 1975. Group selection, sex, and fossils. *Evolution* 29:87–94.

Vidal, N., and S. B. Hedges. 2002. Higher-level relationships of snakes inferred from four nuclear and mitochondrial genes. *Compt. Rend. Biol.* 325:977–985.

Vidal, N., A. S. Delmas, P. David, C. Cruaud, A. Coujoux, and S. B. Hedges. 2007. The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. *Compt. Rend. Biol.* 330:182–187.330:182–187.

Vidal, N., W. R. Branch, O. S. G. Pauwels, S. B. Hedges, D. G. Broadley, M. Wink, C. Cruaud, U. Joger, and Z. T. Nagy. 2008. Dissecting the major African snake radiation: a molecular phylogeny of the Lamprophiidae Fitzinger (Serpentes, Caenophidia). *Zootaxa* 1945:51–66.

Vidal, N., Rage, J.-C., Couloux, A., and S. B. Hedges. 2009. Snakes (Serpentes). Pp. 390–397 *in*: The Timetree of Life (S. B. Hedges and S. Kumar, eds.) The timetree of life. Oxford University Univ. Press, New York.

Vidal, N., J. Marin, M. Morini, S. Donnellan, W. R. Branch, R. Thomas, M. Vences, A. Wynn, C. Cruaud, and S. B. Hedges. 2010. Blindsnake evolutionary tree reveals long history on Gondwana. *Biol. Lett.* 6:558–561.

Vitt, L. J., and J. P. Caldwell. 2009. *Herpetology*. Elsevier, Burlington, MA.

Vuilleumier, F. 1984. Faunal turnover and development of fossil avifaunas in South America. *Evolution* 38:1384–1396.

Waldron, A. 2010. Lineages that cheat death: surviving the squeeze on range size. *Evolution* 64:2278–2292.

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.

Wiens, J. J. 2011. The causes of species richness patterns across space, time, and clades and the role of “ecological limits”. *Q. Rev. Biol.* 86:75–96.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* 19:639–644.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Ann. Rev. Ecol. Evol. Syst.* 36:519–539.

Wiens, J. J., C. A. Kuczynski, S. A. Smith, D. G. Mulcahy, J. W. Sites, T. M. Townsend, and T. W. Reeder. 2008. Branch lengths, support, and congruence: testing the phylogenomic approach with 20 nuclear loci in snakes. *Syst. Biol.* 57:420–431.

Wiens, J. J., C. A. Kuczynski, T. Townsend, T. W. Reeder, D. G. Mulcahy, and J. W. Sites, Jr. 2010. Combining phylogenomics and fossils in higher level squamate reptile phylogeny: molecular data change the placement of fossil taxa. *Syst. Biol.* 59:674–688.

Yoder, J. B., E. Clancey, S. Des Roches, J. M. Eastman, L. Gentry, W. Godsoe, T. J. Hagey, D. Jochimsen, B. P. Oswald, J. Robertson, et al. 2010. Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol.* 23:1581–1596.

Zaher, H. 1999. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bull. Am. Mus. Nat. Hist.* 240:1–168.

Associate Editor: S. Magallón

## Appendix

The constant-rates extinction-limited model for stem-group ages presented here is related to the constant-rate models presented by Rabosky (2010a) and others. First, the hL of clades is empirically determined by maximizing the correlation between age ( $t$ ) and diversity ( $n$ ) among the extant clades (e.g., Fig. 5), which should include the peak of observed diversity for extant lineages. Thus, for clades  $t < \text{hL}$ , the likelihood is simply the standard birth–death likelihood (Nee et al. 1994; Bokma 2003) for the data ( $D$ ):

$$L_1(D | r, \varepsilon) = \prod_{i=1}^N Pr(n_i | r, \varepsilon, t_i), \quad (\text{A1})$$

where

$$Pr(n_i | r \cdot \varepsilon \cdot t_i) = (1 - \beta) \beta_i^{n_i - 1} \quad (\text{A2})$$

and

$$\beta_i = \frac{e^{r t_i} - 1}{e^{r t_i} - \varepsilon}. \quad (\text{A3})$$

Maximizing this likelihood and calculating  $r_0 (>0)$  and  $\varepsilon_0 (<1)$  for clades  $t < \text{hL}$  also yields the expected number of species at hL ( $E\{\text{sp}\} = e^{r_0 \text{hL}}$ ). Thus for clades  $t > \text{hL}$ , the likelihood of the deterministic-extinction model ( $r_1 < 0, \varepsilon_1 > 1$ ), conditioned on the the time elapsed since the half life ( $t c_i = t_i - \text{hL}$ ) and the expected number of species ( $E\{\text{sp}\}$ ), is

$$L_2(D | r, \varepsilon) = \prod_{i=1}^N Pr(n_i | r, \varepsilon, t c_i, E\{\text{sp}\}), \quad (\text{A4})$$

where the right-hand term is given by Raup (1985), corrected by Foote et al. (1999):

$$\begin{aligned} Pr(n_i | r \cdot \varepsilon \cdot t c_i \cdot E\{\text{sp}\}) = & \sum_{j=1}^{\min(E\{\text{sp}\}, n_i)} \binom{E\{\text{sp}\}}{j} \binom{n_i - 1}{j - 1} \\ & \times \alpha_i^{E\{\text{sp}\} - j} [(1 - \alpha_i)(1 - \beta_i)] \beta_i^{n_i - j}, \end{aligned} \quad (\text{A5})$$

where  $\beta$  is defined above and

$$\alpha_i = \varepsilon \beta_i \quad (\text{A6})$$

as given by Bokma (2003) and Rabosky et al. (2007). This is conditioned on the survival of the clades by dividing by  $(1 - \alpha^{E\{\text{sp}\}})$ . Thus, the likelihood of a set of clades under the extinction-limited model is  $\ln L = \ln L_1 + \ln L_2$ , which, given the empirical half life of clades, yields a four-parameter model with the initial birth–death rates  $r_0 > 0$  and  $\varepsilon_0 < 1$ , and the secondary death–birth rates  $r_1 < 0$  and  $\varepsilon_0 > 1$ . Future generalizations of this model could allow for a relaxed distribution of rates, such that they can vary among clades (e.g., Rabosky 2010a,b).

## *Supporting Information*

The following supplementary material is available for this article:

**Appendix S1.** GenBank accession numbers, genes, and species used in the molecular dataset.

Supporting Information may be found in the online version of this article.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.