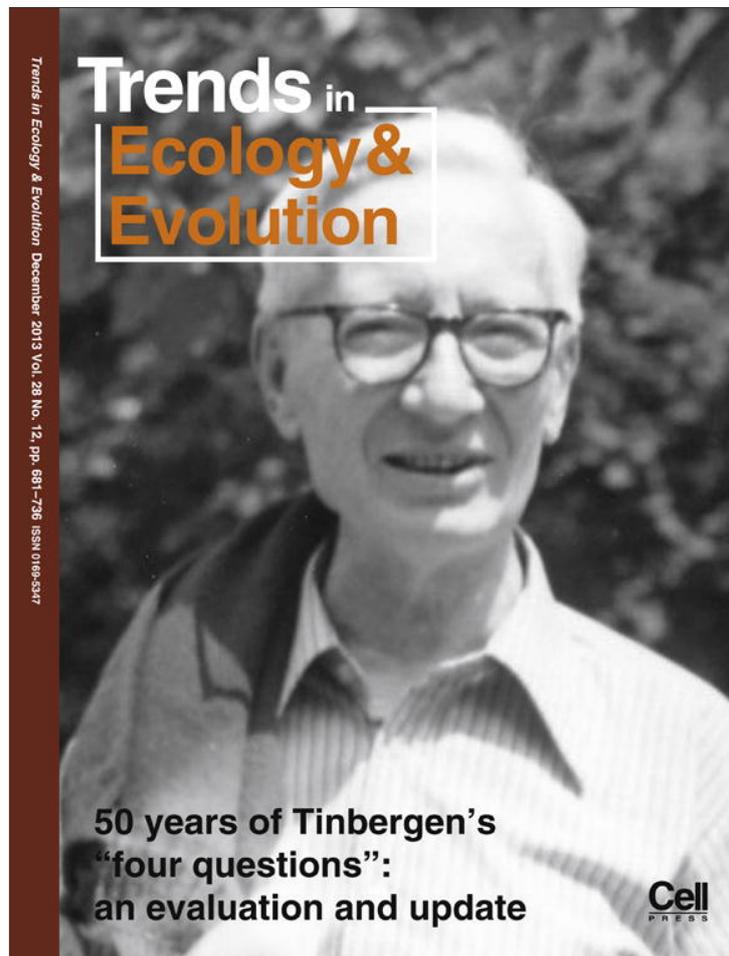


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>

Phylogenetic estimates of speciation and extinction rates for testing ecological and evolutionary hypotheses

R. Alexander Pyron¹ and Frank T. Burbrink^{2,3}

¹ Department of Biological Sciences, The George Washington University, 2023 G St. NW, Washington, DC 20052, USA

² Department of Biology, The Graduate School and University Center, The City University of New York, 365 5th Avenue, New York, NY 10016, USA

³ Department of Biology, The College of Staten Island, The City University of New York, 2800 Victory Boulevard, Staten Island, NY 10314, USA

Phylogenies are used to estimate rates of speciation and extinction, reconstruct historical diversification scenarios, and link these to ecological and evolutionary factors, such as climate or organismal traits. Recent models can now estimate the effects of binary, multistate, continuous, and biogeographic characters on diversification rates. Others test for diversity dependence (DD) in speciation and extinction, which has become recognized as an important process in numerous clades. A third class incorporates flexible time-dependent functions, enabling reconstruction of major periods of both expanding and contracting diversity. Although there are some potential problems (particularly for estimating extinction), these methods hold promise for answering many classic questions in ecology and evolution, such as the origin of adaptive radiations, and the latitudinal gradient in species richness.

Macroevolutionary inference

Estimating rates of diversification [speciation (λ) and extinction (μ); see [Glossary](#)] provides the basic structure for answering many fundamental questions in biology, relating various properties of organisms and their environments to these rates [1,2]. Questions include: are speciation and extinction correlated with biogeographic areas, explaining patterns such as latitudinal diversity gradients [3,4]? Are diversification rates related to morphological evolution and can they explain rapid diversification during adaptive radiations [5,6]? Are long-term speciation and extinction rates determined by population-level factors, such as reproductive isolation and sexual selection [7,8]? Phylogenetic estimates can also help one

understand how life-history adaptations affect speciation and extinction in response to climatic variation [9], and even predict future extinction risks due to climate change [10].

The lack of robust mathematical models for estimating speciation and extinction rates from phylogenies previously limited such estimates. Initially, the age and diversity of a clade provided the only information about speciation and extinction [11]. However, it is now accepted that branch lengths and topology information from phylogenies yield more precise rate estimates [12]. The past 5 years have seen a proliferation of models for estimating rates from

Glossary

Diversification process: the tempo and mode of diversification in a group; variation in speciation and extinction rates through space and time and across lineages.

Diversity dependence: the species-level generalization of DD from population biology; a fixed amount of resources limits the number of coexisting entities. Thus, speciation declines and extinction increases as more species compete for fewer resources.

Ecological opportunity: the open niche space (resource availability) for organisms to exploit; typically increased by colonization of new areas, extinction of competitors, or key innovations.

Extinction: global loss of species from a phylogeny, measured in lineages \times my^{-1} .

Pull of the present: a phylogenetic signature of extinction on dated trees, where the removal of older branches gives the appearance that more speciation events have occurred recently.

Rate estimator: algorithms for estimating speciation and extinction rates from diversity and age data from fossils (clade based), or branch-length information from trees (phylogeny based).

Speciation: evolutionary divergence of lineages in a phylogeny, measured in lineages \times my^{-1} .

Species tree: the 'true' organismal phylogeny, which can be most powerfully estimated using coalescent information from multiple independent genealogies (gene trees).

Time dependence: variation in speciation and extinction over time caused by external factors, generalizing specific processes such as diversity or trait dependence.

Trait dependence: the correlation of speciation and extinction rates with an organismal trait; for example, smaller body size or complexity of breeding plumage may promote more rapid diversification.

Turnover: replacement of lineages through time due to extinction and speciation, at similar levels of diversity. Higher relative extinction fractions ($\mu/\lambda = \epsilon$) indicate higher turnover.

Corresponding author: Pyron, R.A. (rpyron@colubroid.org).

Keywords: phylogenies; systematics; comparative methods; speciation; extinction; diversity dependence; traits; ecology; evolution.

0169-5347/\$ – see front matter

© 2013 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.tree.2013.09.007>



time-calibrated phylogenies of extant taxa. Major innovations include models that allow both rates to change continuously through time [13–15], with respect to the diversity of the clade [16,17], or with regard to character states, whether continuous, discrete, or biogeographic [18–21]. Recently, some models have linked multiple processes, such as key innovations that decouple DD among clades [17].

These models also have the major advantage of reconciling phylogenetic estimates of diversification with the fossil record. Many early estimates suggested that extinction had not occurred at all, even in clades with fossil records [22]. Early models also did not allow negative net diversification rates, where speciation rates are lower than extinction rates [23], although this was mathematically and conceptually possible [12]. Relaxing this restriction computationally has revealed strong support for the signature of extinction in molecular phylogenies, matching the patterns found in the fossil record [13]. Similarly, accounting for DD in speciation and extinction yields robust estimates of extinction corroborated by fossil estimates [17]. Although the methods are relatively new, speciation and extinction rates can also be estimated relatively accurately from phylogenies containing extinct and extant taxa [24,25], based on molecular and morphological data [26,27].

The development and scrutiny of diversification models has also begun to reveal some limitations. Many different processes can yield similar patterns in extant phylogenies, obscuring the true process and yielding inaccurate rate estimates [28–31]. Genealogical discordance (i.e., gene trees that do not match the species tree) can result in erroneous inferences of declining speciation rates and early bursts of diversification [32]. Other factors, such as cryptic diversity and other unaccounted-for speciation processes, can mislead diversification-rate estimates [33,34]. Here, we give an overview of: (i) methods for estimating speciation and extinction rates developed over the past 5 years (with a description of the computer package implementing them, where applicable); (ii) potential sources of error in those estimates; and (iii) applications of these methods to fundamental questions in ecology and evolution.

Phylogenetic models of speciation and extinction

A time-calibrated phylogeny is a collection of speciation events, which are defined by their time of origin (branching time) and time of persistence (branch length), and of extinction events, which mark the termination of lineages at some point in the past [12]. Extinctions may be observed (i.e., a fossil species is present in the tree), in which case some branches terminate before the present, or unobserved and, thus, inferred based on their effects on the branch lengths subtending extant taxa (Figure 1). Therefore, the distribution of branch lengths can be related to time, diversity, or traits, based on how the branches are observed to lengthen or shorten in response to those variables.

The distribution of speciation times in a reconstructed phylogeny differs in a predictable way from the complete phylogeny (Figure 1A). For example, a constant rate of extinction will prune young and old branches with equal probability. However, when an older branch is pruned, this lengthens the reconstructed branch connecting the remaining taxa to the root (Figure 1A,B) proportionally

more than for a younger branch. This results in a higher density of younger nodes, known as the ‘pull of the present’ [12]. For a clade of a given age with constant extinction, a lower speciation rate will yield fewer taxa subtended by longer branches, whereas a higher rate will yield more taxa subtended by shorter branches. Higher extinction rates will yield shorter branches closer to the present (Figure 1C). Conversely, longer branches subtending terminal taxa with shorter branches early in the tree (Figure 1C) often indicate a decline in speciation rate with a constant rate of extinction [15], because high early rates yield short older branches.

The basic likelihood of a phylogeny (see [1]) under a given diversification model is the product of the probability of observing the terminal branches: the probability that N species arose in T time, multiplied by the probability that each of the $2N - 1$ branches persisted for the observed length of time t_i without either diverging again or going extinct. Under a birth–death (λ and μ) model [35], likelihoods can be conditioned on the observation of both speciation and extinction events (Figure 1A) on a phylogeny [24,25,36,37], or on the survival of the phylogeny to the present day (Figure 1B) and the observation of only extant species [12,14,38]. Dated molecular phylogenies are the most common in practice and, in this case, branches begin at a speciation event and terminate either at the present or a subsequent speciation event (Figure 1C). Many models assume that all topologies are equally probable [39], although some models can account for expected topological imbalances due to processes such as heritable extinction rates or protracted speciation events [29,33].

Time-dependent rates of speciation and extinction

Temporal variation in rates due to external factors (e.g., changing environmental conditions) may cause diversification rates to shift drastically over the lifetime of a clade [40]. Although the likelihoods for time-dependent rates had been derived by previous authors [12], they were not implemented in usable packages until recently [41]. In contrast to early algorithms, estimates of speciation and extinction no longer have to be constant across the phylogeny [1,12]. Variable speciation and extinction rates can be estimated either as discrete rate shifts through time and along branches [42–46], or with continuously time-dependent models [15,47], such as an exponential decrease in speciation rate over time [15].

New parameterizations introduced by Morlon and others also explicitly model negative net diversification rates ($\lambda - \mu < 0$) and, thus, account for periods of both expansion and contraction in diversity (Box 1), providing a closer fit to the fossil record [13,42,48]. These implementations can explicitly recover periods of declining diversity, with extinction exceeding speciation. Clades with negative diversification may be rare (because they will quickly go extinct in most cases), but are supported by the fossil record in some instances [13,23]. Other modifications account for incomplete sampling of phylogenetic trees [12,46,49,50]. With these models [13,42], speciation and extinction rates are specified as arbitrary functions of time (e.g., linear or exponential), and subclades can have diversification rates decoupled from the main tree [13,51],

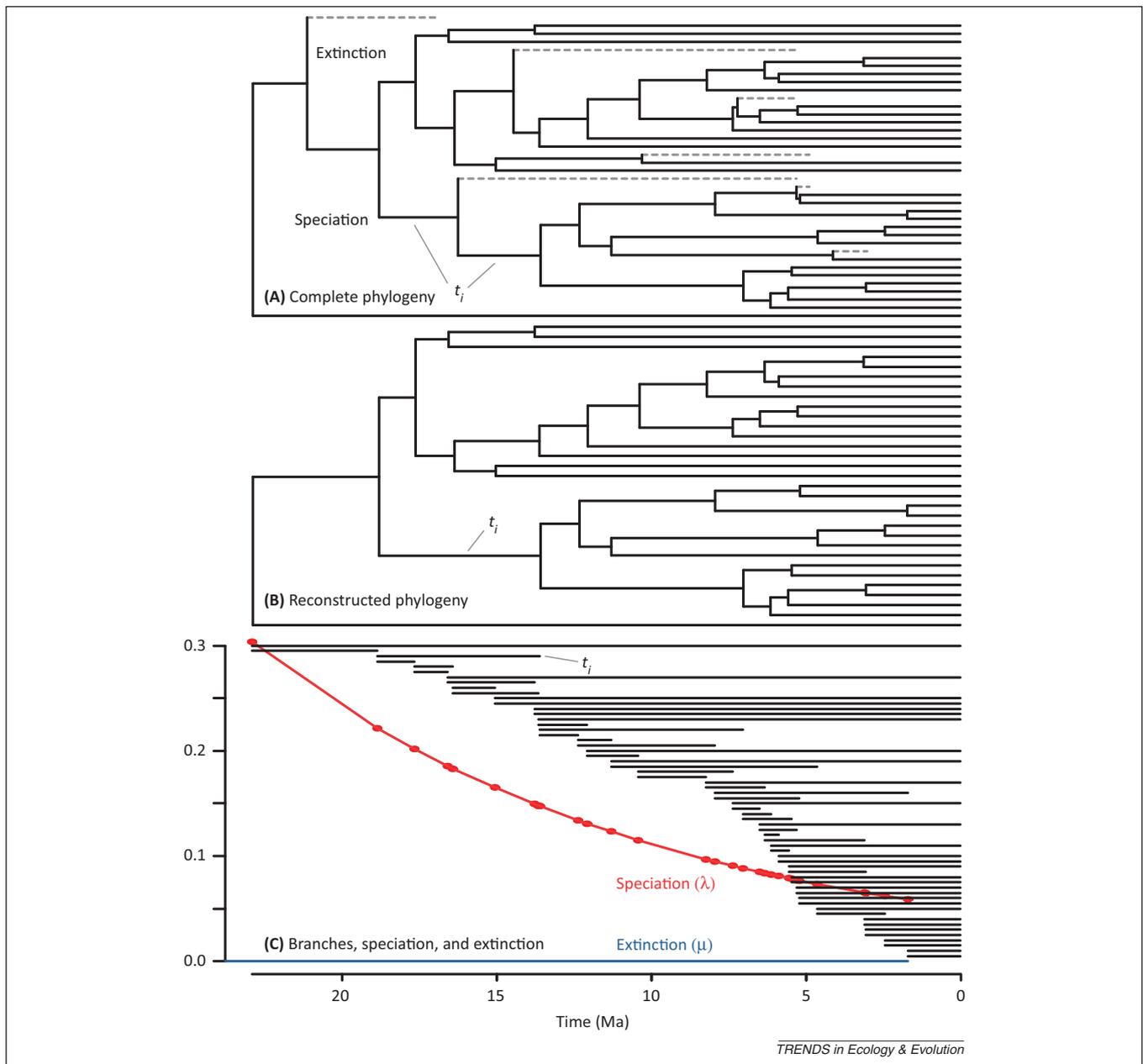


Figure 1. The birth–death process estimated from a phylogeny. **(A)** A complete phylogeny, containing seven extinct and 31 extant lineages [24]. Thus, speciation and extinction events can be observed and rates calculated directly [24,25,36]. Although this type of phylogeny is rare, new methods make it an increasing possibility for data sets combining fossil and molecular data [26,27]. **(B)** The reconstructed phylogeny, containing only 31 extant lineages, where the branches t_i indicated in (A) are collapsed into a single branch t_i . Numerous likelihood expressions exist for estimating speciation and extinction conditioned on the number of taxa (N), root age (T), and branch lengths (t) [38]. **(C)** Distribution of branch lengths and a best-fit time-dependent model [52] showing exponential decline in speciation rate (from 0.3 lineages \times my^{-1} to 0.06), and constant extinction (0.001 lineages \times my^{-1}), which underestimates the actual value of 0.017 [24]. For (B), a diversity-dependent model without extinction provides a better fit [52], but is contradicted by the fossil record (A), which contains known fossil taxa [24].

allowing diversification to vary in different lineages (in different areas, for example). However, it may be difficult to avoid overfitting such models, and simulations should be used to determine the validity of highly parameterized historical scenarios [45,46].

Diversity dependence in diversification

Clade diversity may also have a strong role in causing diversification rates to change over time (Box 2) if ecological factors exert feedback on rates of speciation and extinction, possibly as increasing species richness saturates available

niches [52–55]. Several techniques model this explicitly [16,17], yielding estimates of carrying capacity (K). A fundamental problem for calculating these effects is that DD in speciation rates can be easily extracted from a phylogeny of extant taxa, but incorporation of extinction requires inference of unobserved taxa in the past that also influenced rates [56,57]. A solution recently proposed by Etienne and colleagues for this problem involves the use of hidden Markov models (HMM) to estimate the likelihood of extinction and speciation (DD + E) under DD (in the R package ‘DDD,’ [17]) while integrating over unobserved extinction events.

Box 1. Time-dependent rates of speciation and extinction

An initial expansion and subsequent contraction in species richness is a common pattern found in diversification studies (particularly in the fossil record), necessarily exhibited by all extinct groups, and by many extant groups [23]. This implies that negative net diversification rates have been relatively common throughout the tree of life [23,28]. However, commonly used models constrain speciation rates (λ) to be greater than extinction rates (μ), yielding positive net diversification rates ($\lambda - \mu; r$), and relative extinction fractions ($\mu/\lambda; \epsilon$) less than 1 [14,42,44] (Figure 1). Although the initial formulation of the birth–death process applied to phylogenies included explicit methods for incorporating time-dependent and negative diversification [12], only recently have these been implemented by Morlon and colleagues [13], providing greater reconciliation with the fossil record. These models allow λ and μ to be specified as arbitrary functions of time [commonly linear or exponential (shown)], so that periods of both increasing and decreasing diversity can be recovered. A drawback of these models is that they neither account for the potential effects of trait dependence on evolutionary rates, nor allow rates to vary continuously across branches. Rate variation can be evaluated by decoupling the rates of a subclade and estimating two (or more) time-dependent functions for λ and μ [13].

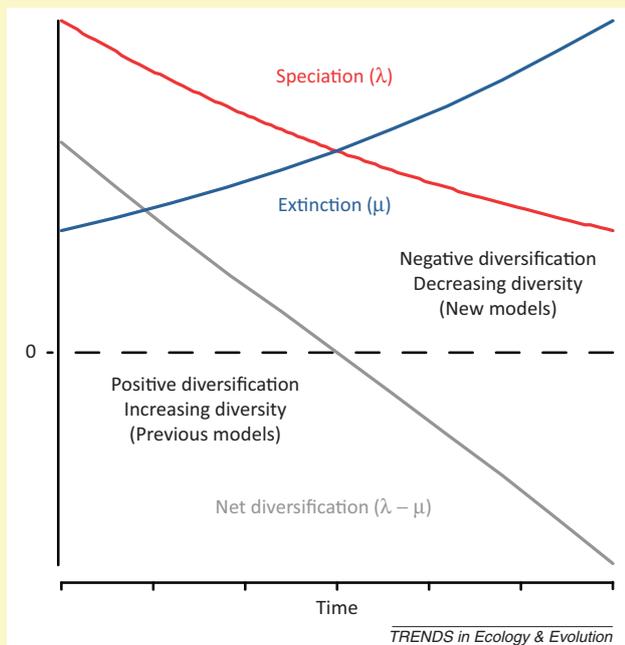


Figure 1. Illustration of exponential declines in speciation rate (λ) and increases in extinction rate (μ) that intersect, yielding an initial increase in diversity and subsequent decrease with negative net diversification rates.

Box 2. Diversity dependence in speciation and extinction

The idea that increasing diversity in regions (and, thus, presumably, increasing interspecific interactions as species compete for declining resources) would affect diversification is an old one [53,54,92–95]. However, only recently did Rabosky and Lovette introduce an explicit model for detecting DD in completely sampled molecular phylogenies [16], in the R package ‘laser’ [41]. When extinction is assumed to be zero, this can easily be observed as a lengthening (either linearly or exponentially) of waiting times between speciation events as the number of branches increases, yielding estimates of total carrying capacity (K) in clades and initial speciation rates (λ_0) (Figure 1). This can be tested against a null model of monotonic decay in speciation rate, such as if speciation were being modulated by external ecological controls [16]. However, extinction is not zero for most clades, which can have a strong effect on estimates of λ and K . The difficulty arises in estimating the effects of extinct taxa on historical rates, when they are not observed in the phylogeny. Etienne *et al.* use a HMM to integrate stochastically across extinction and speciation, while allowing for DD in both [17], in the R package ‘DDD,’ allowing for incomplete sampling. From this, one can estimate both realized carrying capacities (K) in the presence of extinction, and potential carrying capacities in the absence of extinction ($K' = \lambda_0 K / (\lambda_0 - \mu)$). This model typically assumes decay in speciation and increases in extinction, but any model can be accommodated.

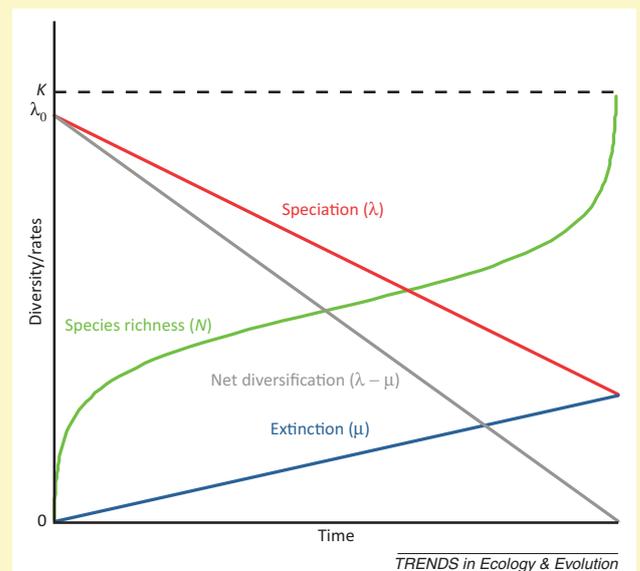


Figure 1. Illustration of diversity dependence with extinction, resulting in an ‘inverted S’ shape of diversity through time [17]. This model allows for estimation of K (carrying capacity), and diversity dependence in speciation (λ), extinction (μ), or both (as shown).

DD now seems to be an overwhelmingly common feature of empirical phylogenies [17,58,59], confirming predictions from ecological theories of adaptive radiation that rapid saturation of available niche space reduces diversification rates [17,53,58]. This is typically interpreted as the effects of increasing diversity leading to declining niche volume and increasing interspecific interactions limiting speciation and increasing extinction [17,60]. It is important to note that DD is in essence a special case of time-dependent models, where the temporal change is linked to clade richness. Differences between these models have not yet been thoroughly explored.

Additionally, the mechanisms by which DD changes diversification rates are not well defined at present.

Further considerations not parameterized by current models are the effects of other clades (i.e., competitor diversity [61]), amount of available resources (i.e., ecological opportunity [62]) and the potential effect of unsampled species due to protracted diversification [33] or cryptic speciation (see below). Some studies have tested time-dependent carrying capacities (as ecological opportunity shifts through time, such as after mass extinctions), but these were not well supported [51].

Trait-dependent rates

Dependence of speciation and extinction rates on organismal traits is an old idea in evolutionary biology generally [63]. The link between character states and rates of

Box 3. Trait dependence in speciation and extinction

Trait evolution and species diversification are not always independent. Species with different traits, whether discrete, such as limb number; continuous, such as body size; or extrinsic, such as geographic area, may have different rates of speciation and extinction related to those variables [65]. This can lead to serious biases if evolutionary rates and character histories are estimated assuming independence, but new models allow these factors to be untangled [66]. Maddison and colleagues introduced a model (Figure 1) in which speciation and extinction rates vary according to the state of a binary character (BiSSE [18]), which has now been extended to multistate (MuSSE) and continuous (QuaSSE) characters, and allows for incomplete sampling [19,49]. Another extension also treats geographic range similarly (GeoSSE [21]), although only two areas are supported at present. Other models extend the BiSSE framework to test for punctuated equilibrium (i.e., speciation changes) versus gradualism (BiSSE-ness [67]).

However, some drawbacks remain to these models. One is that current implementations (e.g., the R package 'diversitree' [20]) do not easily support the analysis of multiple traits simultaneously, although this is easily altered in the general framework and will likely be added in the future [19]. Thus, one must be careful not to estimate multiple sets of speciation and extinction rates for a single clade, which are difficult to interpret biologically. Also, results may be dominated by one or a few clades that are particularly diverse and exhibit a specific trait value and, thus, the apparent effect size of a significant relation between a trait and diversification may be inflated.

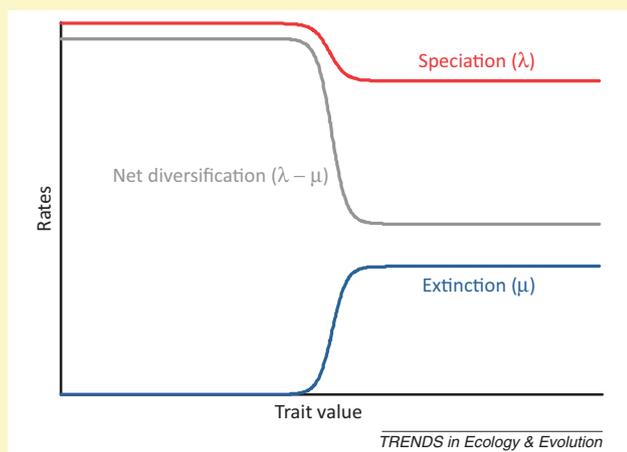


Figure 1. Example of a sigmoidal relation between speciation (negative) and extinction (positive) and a continuously valued trait (e.g., body size), resulting in greater diversification of clades that have lower values of that trait due to their higher net diversification rate.

speciation and extinction [64,65] can now be modeled explicitly (Box 3). If an intrinsic trait (e.g., body size) affects the probability that a lineage will diversify or go extinct, this in turn may impact estimates of speciation and extinction, and the character history (i.e., ancestral state estimates) [66]. New models introduced by Maddison, FitzJohn, Goldberg, and colleagues in the R package 'diversitree' integrate the likelihood framework for speciation and extinction described above with existing models for character-state change [65]. These evaluate the effect of binary and multistate [18,20,49], continuous [19], and geographic [21] traits on diversification. Recent extensions also allow for branch- versus node-based changes, providing estimates of changes along branches, at speciation events, and independent state-based estimates [67]. This

ultimately enables one to determine whether organismal attributes affect diversification rates [5,21].

Future directions

An immediate limitation of all three types of model (linking rates either to time, diversity, or traits) is that they are not fully integrated; a complete theory of ecomorphological diversification includes roles for trait-dependent speciation and extinction, which also varies with respect to existing species richness and available niches, and changes over time [51,68]. Nevertheless, available models allow for a great degree of integration. Some adaptive radiation models allow for time-dependent carrying capacities, and model rate variation in decoupled subclades expressing key innovations [51]. Approaches recently introduced by Rabosky and colleagues model multiple concurrent time-dependent processes that can change continuously across the phylogeny, and integrate rates of trait evolution [6,7]. Allowing time-dependent rates in trait-dependent models is mathematically possible, and is a simple matter of programming. Additionally, these algorithms do not accommodate trees with both extinct and extant terminals [19,24,37], although extending them to include fossils should be conceptually straightforward.

Can speciation and extinction be reliably estimated from phylogenies?

Assuming that the phylogeny is known completely how confident can one be in the estimates of speciation and extinction using the models listed above? Phylogeny-based estimators of speciation rate appear to perform well under most empirical conditions, because the distribution of branch lengths and branching times provides more information for extracting diversification information than do age and diversity alone (but see [28]).

Simulations and empirical tests

Tests of the recently proposed time-dependent models [13,42] indicate apparently good power to detect both constant extinction with decreasing speciation, and constant speciation with increasing extinction, even on relatively small trees (<100 tips). In one set of simulations using trait-dependent models, power to detect a sigmoidal relation between speciation rate and a continuous trait varied from 10% to 40% for 125-taxon trees when the magnitude of the effect was weak, to over 70% for 500-taxon trees when the effect was strong [19]. For DD models incorporating extinction, the power to detect DD is low at recent timescales, but accuracy and precision increases for older clades showing a strong influence of DD over time [17]. Importantly, the time-dependent and DD + E models both show strong concordance with patterns observed directly from the fossil record in several groups [13,17].

The situation for estimating extinction is not as promising. For trees including fossils, the power to estimate extinction is high [24,25]. By contrast, estimators using only using clade age and diversity data are nearly useless under empirical conditions, almost exclusively yielding estimates of 0 or 1 for relative extinction fraction (μ/λ). This led to suggestions that 'extinction rates should not be estimated from molecular phylogenies' [22]. This is

concerning, because extinction affects other parameters, such as λ and K [17], even if models have good power to estimate them in the absence of extinction. The phylogeny-based estimators perform better, but with wide confidence intervals, and a positive bias in estimated extinction as among-lineage rate variation increases. However, these simulations were run on small trees (50 tips), and did not incorporate time dependence, trait dependence, or DD in extinction rates.

For trait-dependent models, power to estimate extinction is low but not zero, and the effects of a trait on extinction can be recovered approximately 40% of the time on trees with at least 500 tips when the magnitude of the effect is high, although power is lower (nearing 0%) when effect sizes and trees are smaller [19]. As noted above, the time- and density-dependent models recover extinction rates in accordance with the fossil record for the data sets that have been tested, as well as in simulation [13,17]. For trees that include extinct species as terminals, rates of extinction can be observed and quantified more directly and accurately [24,25,37], although such data sets are only now beginning to become available [26,27].

Numerous empirical studies have now begun to recover non-zero and biologically plausible estimates of extinction using time-, diversity-, and trait-dependent models [9,13,17,51,60]. It seems reasonable to be cautiously optimistic that the broad-scale signature of extinction can be recovered from well-sampled phylogenies, although extensive simulations are still needed to determine the range of conditions under which rates can be accurately estimated using time-, diversity-, and trait-dependent models. Importantly, extinction estimators seem to be more sensitive to model violation than do speciation estimators [22].

Errors from phylogenetic inference

Accounting for error introduced by gene-tree discordance, unsampled taxa, and cryptic diversity is also likely to improve rate estimates. Simulations suggest that these are critical factors for accurate rate estimates and often plague empirical data sets [34], leading to biased inferences about diversification processes [32]. Given that gene-tree divergences always pre-date species divergences, and the relative magnitude of this effect is greatest at younger nodes, the estimated speciation times and branch lengths from gene trees can exhibit significant skew [69,70]. This results in severe biases towards estimating early bursts of speciation and rate slowdowns in both simulated and empirical phylogenies [32]. Accounting for coalescent variance in branch lengths during tree inference is crucial for accurate estimation of rates, and failure to do so may be a primary reason why many studies show early bursts of diversifications.

Similar problems are posed by unsampled diversity. Although incomplete sampling can be easily accounted for using time-, diversity-, and trait-dependent frameworks and existing algorithms [12,13,17,19,49], these assume that the total diversity of the group is known with a relative degree of accuracy. Errors in the sampling fraction change expectations for the density of nodes and lengths of branches, biasing rate estimates. Even for relatively well-known groups, such as frogs, new species are accumulating at a

massive rate, and previous estimates of total richness were drastically underestimated [71,72]. One way of addressing this may be to run models under various sampling fractions, to determine whether this parameter is dominating results. Finally, cryptic diversity within described species may also exert a strong effect, because the lack of these lineages also skews the expected distribution of branching times. This results in the same erroneous inference of early bursts as the failure to include known species [73].

Evolutionary and ecological applications

Estimating speciation and extinction rates alone is rarely the primary focus of evolutionary investigations. These new models now enable one to investigate some of the fundamental questions in evolutionary biology, such as how variation in speciation and extinction affects biodiversity through space and time, and how ecological factors influence these processes [1,74,75]. Indeed, many of these models were introduced to characterize the shape of evolutionary radiations and the rate processes that generated them [15]. Trait-dependent models can reveal the relations between life-history strategies and diversification [9,76]. Time-dependent models are also useful for testing explicit hypotheses regarding the timing of radiations or extinctions, such as coincidence with the Cretaceous–Tertiary (K–T) boundary [42,77–79].

Diversity- and trait-dependent models are also important for testing some of the fundamental questions regarding adaptive radiation and the effects of ecological opportunity [53,80] for lineages encountering sources of open niche space, such as key innovations [18,51] and colonization of new areas [21,81]. DD seems to occur commonly across the tree of life [16,58,82]. Less is known about how rates of extinction change during adaptive radiation, which can now be tested using models incorporating variable extinction rates [17]. A remaining drawback of these methods is that they do not easily incorporate information about the diversity of other clades (i.e., competitors) or available resources (i.e., total amount of ecological opportunity) and, thus, are likely to be limited in their capacity for inferring complex dynamics [51].

These models can also be used to investigate patterns such as the latitudinal diversity gradient [83]. For instance, biogeographic models can determine whether regional variation in species richness is caused by differences in speciation and extinction rate [81], and trait-dependent models can test whether these rates vary latitudinally in response to environmental factors, such as climate or ecosystem energy [60]. Trait-dependent speciation models could also be used to test hypotheses about species selection if particular characters are correlated with speciation or extinction rates [84]. Finally, punctuated-equilibrium models of trait change can determine whether phenotypic changes affecting speciation and extinction rates are clustered around speciation events, or occur along branches [67,85–88].

Concluding remarks

Biodiversity varies through space and time and among lineages in response to many factors, including external events, such as asteroid impacts and the breakup of

continents; interspecific interactions, such as competition for available niches; and inter- and intraspecific variation in traits, such as body size. These act to affect species richness by changing speciation and extinction rates in different clades over time. This is reflected in both the fossil record and phylogenies of extant taxa, but only recently have models for the latter become available that enable one to estimate these rates directly [1,89]. Despite some limitations [22,28], phylogenies appear to have at least some power to estimate absolute rates of both speciation and extinction. Importantly, models that incorporate negative net diversification rates and allow for periods of contracting diversity within clades align molecular rate estimates with observed patterns in the fossil record [13]. Other models now directly account for the effects of time [13,15], intraclade diversity [16,17], and traits [18,19,21] on speciation and extinction rates. These can now be used to investigate the various processes that lead to classically observed patterns in ecology and evolution, such as adaptive radiation [6,51,58], and latitudinal gradients in diversity [60,83,90].

There are several areas for future research, integration, and synthesis. One is the continued combination of fossil and molecular data [3,24,26,27,68,91]. Consideration of issues such as gene-tree discordance, and the inference of accurate species trees will be an increasingly crucial endeavor, as will accurate characterization of biodiversity in terms of unknown and cryptic species [32,33]. Current models offer unparalleled insight into the evolutionary processes of speciation and extinction. Future goals should be models that allow for: (i) continuous among-lineage variation in speciation and extinction; (ii) the effects of extrinsic factors, such as the diversity of other clades; and (iii) integration of time-, diversity-, and trait-dependent functions in a single analytical framework.

Acknowledgments

We thank D. Rabosky, M. Pennell, R. Betancur-R, G. Orti, the GWU Systematics Discussion Group, and an anonymous reviewer for comments. R.A.P. was funded in part by US National Science Foundation (NSF) grant DBI-0905765 and F.T.B. was funded in part by US NSF grant DEB 1257926.

References

- Ricklefs, R.E. (2007) Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* 22, 601–610
- Benton, M.J. and Emerson, B.C. (2007) How did life become so diverse? The dynamics of diversification according to the fossil record and molecular phylogenetics. *Palaeontology* 50, 23–40
- Jablonski, D. *et al.* (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314, 102–106
- Wiens, J.J. and Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* 19, 639–644
- Hugall, A.F. and Stuart-Fox, D. (2012) Accelerated speciation in colour-polymorphic birds. *Nature* 485, 631–634
- Rabosky, D.L. *et al.* (2013) Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nat. Commun.* 4, 1958
- Rabosky, D.L. (2013) Macroevolutionary speciation rates are decoupled from the evolution of intrinsic reproductive isolation in drosophila and birds. *Proc. Natl. Acad. Sci. U.S.A.* <http://dx.doi.org/10.1073/pnas.1305529110>
- Wagner, C.E. *et al.* (2012) Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* 487, 366–369
- Pyron, R.A. and Burbrink, F.T. (2013) Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecol. Lett.* <http://dx.doi.org/10.1111/ele.12168>
- Pincheira-Dinoso, D. *et al.* (2013) The evolution of viviparity opens opportunities for lizard radiation but drives it into a climatic cul-de-sac. *Global Ecol. Biogeogr.* 22, 857–867
- Magallon, S. and Sanderson, M.J. (2001) Absolute diversification rates in angiosperm clades. *Evolution* 55, 1762–1780
- Nee, S. *et al.* (1994) The reconstructed evolutionary process. *Philos. Trans. R. Soc. Lond. B* 344, 305–311
- Morlon, H. *et al.* (2011) Reconciling molecular phylogenies with the fossil record. *Proc. Natl. Acad. Sci. U.S.A.* 108, 16327–16332
- Morlon, H. *et al.* (2010) Inferring the dynamics of diversification: a coalescent approach. *PLoS Biol.* 8, e1000493
- Rabosky, D.L. and Lovette, I.J. (2008) Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* 62, 1866–1875
- Rabosky, D.L. and Lovette, I.J. (2008) Density-dependent diversification in North American wood warblers. *Proc. R. Soc. B* 275, 2363–2371
- Etienné, R.S. *et al.* (2012) Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc. R. Soc. B* 279, 1300–1309
- Maddison, W.P. *et al.* (2007) Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* 56, 701–710
- FitzJohn, R.G. (2010) Quantitative traits and diversification. *Syst. Biol.* 59, 619–633
- FitzJohn, R.G. (2012) Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol. Evol.* 3, 1084–1092
- Goldberg, E.E. *et al.* (2011) Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* 60, 451–465
- Rabosky, D.L. (2010) Extinction rates should not be estimated from molecular phylogenies. *Evolution* 64, 1816–1824
- Pyron, R.A. and Burbrink, F.T. (2012) Extinction, ecological opportunity, and the origins of global snake diversity. *Evolution* 66, 163–178
- Pyron, R.A. and Burbrink, F.T. (2012) Trait-dependent diversification and the impact of palaeontological data on evolutionary hypothesis testing in New World ratsnakes (tribe Lampropeltini). *J. Evol. Biol.* 25, 497–508
- Paradis, E. (2004) Can extinction rates be estimated without fossils? *J. Theor. Biol.* 229, 19–30
- Ronquist, F. *et al.* (2012) A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Syst. Biol.* 61, 973–999
- Pyron, R.A. (2011) Divergence time estimation using fossils as terminal taxa and the origins of lissamphibia. *Syst. Biol.* 60, 466–481
- Quental, T.B. and Marshall, C.R. (2011) The molecular phylogenetic signature of clades in decline. *PLoS ONE* 6, e25780
- Rabosky, D.L. (2009) Heritability of extinction rates links diversification patterns in molecular phylogenies and fossils. *Syst. Biol.* 58, 629–640
- Liow, L.H. *et al.* (2010) When can decreasing diversification rates be detected with molecular phylogenies and the fossil record? *Syst. Biol.* 59, 646–659
- Quental, T.B. and Marshall, C.R. (2009) Extinction during evolutionary radiations: reconciling the fossil record with molecular phylogenies. *Evolution* 63, 3158–3167
- Burbrink, F.T. and Pyron, R.A. (2011) The impact of gene-tree/species-tree discordance on diversification-rate estimation. *Evolution* 65, 1851–1861
- Etienné, R.S. and Rosindell, J. (2012) Prolonging the past counteracts the pull of the present: protracted speciation can explain observed slowdowns in diversification. *Syst. Biol.* 61, 204–213
- Ruane, S. *et al.* (2013) Coalescent species delimitation in milksnakes (genus *Lampropeltis*) and impacts on phylogenetic comparative analyses. *Syst. Biol.* (in press)
- Nee, S. (2006) Birth-death models in macroevolution. *Annu. Rev. Ecol. Syst.* 37, 1–17
- Keiding, N. (1975) Maximum likelihood estimation in the birth-and-death process. *Ann. Stat.* 3, 363–372

- 37 Didier, G. *et al.* (2012) The reconstructed evolutionary process with the fossil record. *J. Theor. Biol.* 315, 26–37
- 38 Stadler, T. (2012) How can we improve accuracy of macroevolutionary rate estimates? *Syst. Biol.* 62, 321–329
- 39 Guyer, C. and Slowinski, J.B. (1993) Adaptive radiation and the topology of large phylogenies. *Evolution* 47, 253–263
- 40 Sloss, L.L. (1950) Rates of evolution. *J. Paleontol.* 24, 131–139
- 41 Rabosky, D.L. (2006) Laser: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evol. Bioinform.* 2, 247–250
- 42 Stadler, T. (2011) Mammalian phylogeny reveals recent diversification rate shifts. *Proc. Natl. Acad. Sci. U.S.A.* 108, 6187–6192
- 43 Hubert, N. *et al.* (2011) Community assembly and diversification in Indo-Pacific coral reef fishes. *Ecol. Evol.* 1, 229–277
- 44 Rabosky, D.L. (2006) Likelihood methods for detecting temporal shifts in diversification rates. *Evolution* 60, 1152–1164
- 45 Rabosky, D.L. *et al.* (2007) Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proc. R. Soc. B* 274, 2915–2923
- 46 Alfaro, M.E. *et al.* (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl. Acad. Sci. U.S.A.* 106, 13410–13414
- 47 Paradis, E. (2011) Time-dependent speciation and extinction from phylogenies: a least squares approach. *Evolution* 65, 661–672
- 48 Hohna, S. (2013) Fast simulation of reconstructed phylogenies under global time-dependent birth-death processes. *Bioinformatics* 29, 1367–1374
- 49 FitzJohn, R.G. *et al.* (2009) Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst. Biol.* 58, 595–611
- 50 Stadler, T. and Bokma, F. (2013) Estimating speciation and extinction rates for phylogenies of higher taxa. *Syst. Biol.* 62, 220–230
- 51 Etienne, R.S. and Haegeman, B. (2012) A conceptual and statistical framework for adaptive radiations with a key role for diversity dependence. *Am. Nat.* 180, E75–E89
- 52 Burbrink, F.T. and Pyron, R.A. (2010) How does ecological opportunity influence rates of speciation, extinction, and morphological diversification in New World ratsnakes (tribe Lampropeltini)? *Evolution* 64, 934–943
- 53 Schluter, D. (2000) *The Ecology of Adaptive Radiation*, Oxford University Press
- 54 Walker, T.D. and Valentine, J.W. (1984) Equilibrium-models of evolutionary species-diversity and the number of empty niches. *Am. Nat.* 124, 887–899
- 55 Phillimore, A.B. and Price, T.D. (2008) Density-dependent cladogenesis in birds. *PLoS Biol.* 6, 483–489
- 56 Rabosky, D.L. and Lovette, I.J. (2009) Problems detecting density-dependent diversification on phylogenies: reply to Bokma. *Proc. R. Soc. B* 276, 995–997
- 57 Bokma, F. (2009) Problems detecting density-dependent diversification on phylogenies. *Proc. R. Soc. B* 276, 993–994
- 58 Burbrink, F.T. *et al.* (2012) Evidence for determinism in species diversification and contingency in phenotypic evolution during adaptive radiation. *Proc. R. Soc. B* 279, 4817–4826
- 59 Scantlebury, D.P. (2013) Diversification rates have declined in the Malagasy herpetofauna. *Proc. R. Soc. B* 280, 1766
- 60 Pyron, R.A. and Wiens, J.J. (2013) Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proc. R. Soc. B* 2013, 1622
- 61 Betancur-R, R. *et al.* (2012) Apparent signal of competition limiting diversification after ecological transitions from marine to freshwater habitats. *Ecol. Lett.* 15, 822–830
- 62 Yoder, J.B. *et al.* (2010) Ecological opportunity and the origin of adaptive radiations. *J. Evolution. Biol.* 23, 1581–1596
- 63 Simpson, G.G. (1953) *The Major Features of Evolution*, Columbia University Press
- 64 Paradis, E. (2005) Statistical analysis of diversification with species traits. *Evolution* 59, 1–12
- 65 Maddison, W.P. (2006) Confounding asymmetries in evolutionary diversification and character change. *Evolution* 60, 1743–1746
- 66 Paradis, E. (2008) Asymmetries in phylogenetic diversification and character change can be untangled. *Evolution* 62, 241–247
- 67 Magnuson-Ford, K. and Otto, S.P. (2012) Linking the investigations of character evolution and species diversification. *Am. Nat.* 180, 225–245
- 68 Ezard, T.H.G. *et al.* (2011) Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science* 332, 349–351
- 69 Arbogast, B.S. *et al.* (2002) Estimating divergence times from molecular data on phylogenetic and population genetic timescales. *Annu. Rev. Ecol. Syst.* 33, 707–740
- 70 Edwards, S.V. and Beerli, P. (2000) Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. *Evolution* 54, 1839–1854
- 71 Vieites, D.R. *et al.* (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proc. Natl. Acad. Sci. U.S.A.* 106, 8267–8272
- 72 Meegaskumbura, M. *et al.* (2002) Sri Lanka: an amphibian hot spot. *Science* 298, 379
- 73 Harmon, L.J. *et al.* (2003) Tempo and mode of evolutionary radiation in iguanian lizards. *Science* 301, 961–964
- 74 Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* 7, 1–15
- 75 Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science* 235, 167–171
- 76 Drummond, C.S. *et al.* (2012) Multiple continental radiations and correlates of diversification in *Lupinus* (Leguminosae): testing for key innovation with incomplete taxon sampling. *Syst. Biol.* 61, 443–460
- 77 Meredith, R.W. *et al.* (2011) Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334, 521–524
- 78 Ericson, P.G.P. *et al.* (2006) Diversification of Neoaves: integration of molecular sequence data and fossils. *Biol. Lett.* 2, 543–547
- 79 Venditti, C. *et al.* (2011) Multiple routes to mammalian diversity. *Nature* 479, 393–396
- 80 Glor, R.E. (2010) Phylogenetic insights on adaptive radiation. *Annu. Rev. Ecol. Syst.* 41, 251–270
- 81 Rabosky, D.L. and Glor, R.E. (2010) Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proc. Natl. Acad. Sci. U.S.A.* 107, 22178–22183
- 82 Weir, J.T. and Mursleen, S. (2013) Diversity-dependent cladogenesis and trait evolution in the adaptive radiation of the auks (Aves: Alcidae). *Evolution* 67, 403–416
- 83 Mittelbach, G.G. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* 10, 315–331
- 84 Rabosky, D.L. and McCune, A.R. (2010) Reinventing species selection with molecular phylogenies. *Trends Ecol. Evol.* 25, 68–74
- 85 Rabosky, D.L. (2012) Positive correlation between diversification rates and phenotypic evolvability can mimic punctuated equilibrium on molecular phylogenies. *Evolution* 66, 2622–2627
- 86 Goldberg, E.E. and Igić, B. (2012) Tempo and mode in plant breeding system evolution. *Evolution* 66, 3701–3709
- 87 Bokma, F. (2008) Detection of 'punctuated equilibrium' by Bayesian estimation of speciation and extinction rates, ancestral character states, and rates of anagenetic and cladogenetic evolution on a molecular phylogeny. *Evolution* 62, 2718–2726
- 88 Bokma, F. (2002) Detection of punctuated equilibrium from molecular phylogenies. *J. Evol. Biol.* 15, 1048–1056
- 89 Sanderson, M.J. and Donoghue, M.J. (1996) Reconstructing shifts in diversification rates on phylogenetic trees. *Trends Ecol. Evol.* 11, 15–20
- 90 Jansson, R. *et al.* (2013) What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out-of-the-tropics and diversification rate hypotheses. *Evolution* 67, 1741–1755
- 91 Slater, G.J. *et al.* (2012) Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution* 66, 3931–3944
- 92 Sepkoski, J.J. (1984) A kinetic model of Phanerozoic taxonomic diversity 3: post-Paleozoic families and mass extinctions. *Paleobiology* 10, 246–267
- 93 Sepkoski, J.J. (1979) A kinetic model of Phanerozoic taxonomic diversity 2: early Phanerozoic families and multiple equilibria. *Paleobiology* 5, 222–251
- 94 Sepkoski, J.J. (1978) A kinetic model of Phanerozoic taxonomic diversity 1: analysis of marine orders. *Paleobiology* 4, 223–251
- 95 Valentine, J.W. (1973) *Evolutionary Paleocology of the Marine Biosphere*, Prentice-Hall