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REVIEW

How traits shape trees: new approaches for detecting character state-dependent lineage diversification

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key innovation.

Abstract

Biologists have long sought to understand the processes underlying disparities in clade size across the tree of life and the extent to which such clade size differences can be attributed to the evolution of particular traits. The association of certain character states with species-rich clades suggests that trait evolution can lead to increased diversification, but such a pattern could also arise due other processes, such as directional trait evolution. Recent advances in phylogenetic comparative methods have provided new statistical approaches for distinguishing between these intertwined and potentially confounded macroevolutionary processes. Here, we review the historical development of methods for detecting state-dependent diversification and explore what new methods have revealed about classic examples of traits that affect diversification, including evolutionary dead ends, key innovations and geographic traits. Applications of these methods thus far collectively suggest that trait diversity commonly arises through the complex interplay between transition, speciation and extinction rates and that long hypothesized evolutionary dead ends and key innovations are instead often cases of directional trends in trait evolution.

Introduction

Disparities in clade size are common across the tree of life at all scales, from recent radiations to deep divergences. Understanding the factors that underlie these disparities, and the resulting imbalance in phylogenetic trees, is a central goal in evolutionary biology (Heard & Mooers, 2002; Ricklefs, 2007). Although variation in clade size is expected due to purely stochastic processes (Raup *et al.*, 1973; Slowinski & Guyer, 1989), many groups exhibit an imbalance far beyond what is expected by chance alone (Mooers & Heard, 1997). This suggests that differences in species richness between clades often reflect true differences in speciation and/or extinction rates, which begs the question: what could account for these rate differences? One classic explanation is that some traits are targeted by selection at the species level and that evolutionary transitions in these traits result in fixed differences in net rates of diversification (speciation minus extinction) (Jablonski, 2008; Rabosky & McCune, 2010).

A variety of mechanisms have been proposed to explain how traits could alter diversification rates. For example, some traits are hypothesized to act as key innovations, spurring diversification by opening up new ecological opportunities (Mitter *et al.*, 1988; Hodges & Arnold, 1995). Alternatively, the acquisition of traits that are evolutionary dead ends can increase the likelihood of extinction (Stebbins, 1957). In this view, traits that are targeted by species selection do not evolve passively along the phylogeny but instead prune some branches of the tree while promoting the splitting of others (Maddison, 2006). The scope of traits posited to affect diversification rates is broad, including both biotic factors, such as morphology, physiology, behaviour, ecology and life history characteristics, as well as abiotic factors (e.g. Arnqvist *et al.*, 2000; Mendelson & Shaw, 2005; Phillimore *et al.*, 2006; Wheat *et al.*, 2007; Winkler *et al.*, 2009; Arakaki *et al.*, 2011).

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Despite a long-standing interest in species selection, linking character evolution with shifts in diversification rates has proved challenging for several reasons. First, as is the case with most comparative methods, attributing an effect to a particular character is complicated by the possibility that the character's evolution might be correlated with another trait, for example, due to shared developmental pathways, pleiotropic effects or linkage disequilibrium. This issue is ameliorated, however, in cases where the trait of interest appears many times in different lineages, to some degree randomizing the background on which the trait evolved (Galis, 2001; Ree, 2005).

Another issue relates to the general challenge of linking pattern to process in evolutionary biology because many processes can give rise to similar patterns. In the case of species selection, processes such as directional trait evolution due to asymmetrical transition rates can lead to an abundance of taxa with a particular trait (Nosil & Mooers, 2005), which is the same pattern expected if that trait was associated with higher diversification rates. Although this fundamental challenge has been noted by several authors (e.g. Janson, 1992; Maddison, 2006), new statistical approaches capable of teasing apart these intertwined and potentially confounded processes have only recently emerged (Maddison *et al.*, 2007). Although these new state-dependent diversification (SDD) methods have important implications for reconstructing ancestral character states (Goldberg *et al.*, 2008; Paradis, 2008), our review will focus on their utility for identifying traits that affect diversification and how they do so (e.g. as a key innovation or dead end). Applications of these SDD methods suggest that indeed many apparent evolutionary dead ends and key innovations are instead cases of directional trends in trait evolution, placing new importance on the integration of macro- and microevolutionary studies to understand how and why phenotypic transitions happen within lineages.

History of methods for relating character evolution and diversification

Although the notion that the evolution of particular traits can increase or decrease the success of lineages (in terms of species richness) has a long history in the literature (Miller, 1949; Stebbins, 1957; Stanley, 1975; Van Valen, 1975), statistical tests only began to appear with the availability of large molecular phylogenies in the 1990s. The first tests for character state-dependent diversification were based on sister group comparisons, where standing diversity is compared among clades possessing alternate character states (Sanderson & Donoghue, 1996). The repeated association of differences in sister clade size and the trait of interest serves as evidence for an effect of that trait on diversification rate (Slowinski & Guyer, 1993; Paradis, 2012). Significant results from these sister group comparisons provided support for classic key innovations, such as floral nectar spurs (Hodges & Arnold, 1995), and other factors long hypothesized to drive diversification, such as sexual selection (Barraclough *et al.*, 1995; Mitra *et al.*, 1996).

As a method for testing the effect of traits on diversification, sister group comparisons, whether parametric (Slowinski & Guyer, 1993) or not (Mitter *et al.*, 1988), have two significant limitations. First, these tests only focus on net differences in species richness and therefore cannot address whether traits affect diversification through changes in speciation or extinction rates. This makes them less useful for testing evolutionary dead ends in particular, which are posited to act through increased extinction (Stebbins, 1957). The second and more considerable limitation is the need to begin with a confident ancestral state reconstruction that identifies a single character state change distinguishing the two groups. This is not a trivial issue because many traits of purported adaptive significance have high transition rates, leading to ambiguity in the ancestral states inferred at nodes (Schluter *et al.*, 1997). Ree (2005) attempted to address this challenge by incorporating Bayesian stochastic mapping into tests for SDD, thereby integrating over uncertainty in the number and location of character state changes. This approach provided increased statistical power by allowing the whole tree, rather than selected sister clades with fixed character state differences, to be included in the analysis (see also Chan & Moore, 2002). However, it did not solve the general issue of relying on the reconstruction of trait shifts prior to conducting tests of SDD.

To illustrate the problem, consider the hypothetical example in Fig. 1. The true history of speciation, extinction and character evolution is shown on the left. Although the derived state (black) has arisen many times, it represents an evolutionary dead end and, with time, consistently leads to extinction. However, if we were to sample the extant species in this group without knowing the existence of the many black lineages that had been pruned over time from the tree, we would be likely to incorrectly infer the history of character evolution (Goldberg *et al.*, 2008). Therefore, character evolution cannot be estimated separately from the history of diversification when characters themselves are shaping the tree. Another intuitive way to understand this problem is that a dead end trait (or any other trait that alters diversification rates) biases the distribution of character states in the tips and will therefore violate the assumptions of ancestral state reconstruction methods.

As an exciting solution to these issues, Maddison *et al.* (2007) proposed a new model (the binary-state speciation and extinction or 'BiSSE' model) that simultaneously estimates rates of character transitions and diversification parameters without relying on the reconstruction of ancestral states (Fig. 2b). BiSSE adds

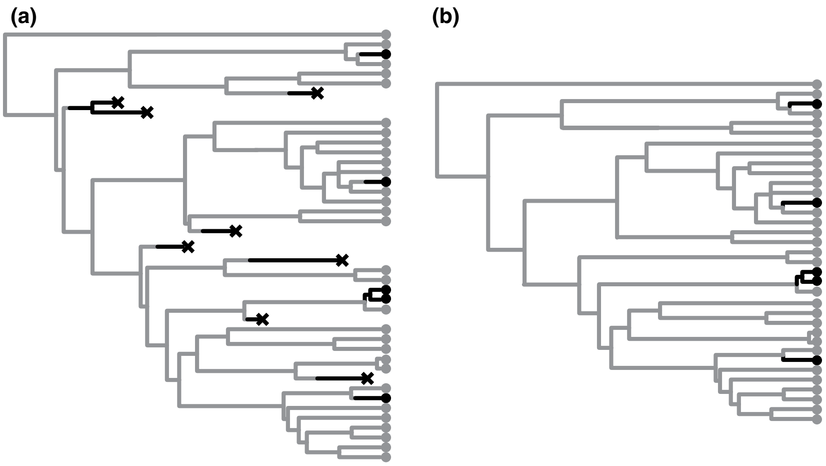


Fig. 1 The interplay of character evolution and lineage history: an example of an evolutionary dead end trait. Extant species have either the ancestral state (grey circles) or the dead end trait (black circles). Black branches represent lineages with the dead end trait, with lineages that have gone extinct depicted with a cross. (a) The true history of the evolution of the dead end trait with all character transitions, speciation and extinction events shown. This history cannot be recovered with common methods (e.g. maximum parsimony [as in (b)] or maximum likelihood with the Mk1 or Mk2 model) that assume that the character has not shaped the tree. In this case, the reconstruction infers many fewer origins of the black state than actually occurred (b).

character state-dependent birth–death (speciation and extinction) parameters to the commonly used continuous time Markov models of trait evolution (Fig. 2; Pagel, 1994; O'Meara, 2012). The BiSSE model can be used to test for SDD by comparing rates of speciation (λ_0, λ_1) and extinction (μ_0, μ_1) in each of the two states of a binary character (0,1). Net diversification in each state can be calculated as the difference between speciation and extinction ($r_0 = \lambda_0 - \mu_0$; $r_1 = \lambda_1 - \mu_1$). Although the original implementation of BiSSE required a complete phylogeny (i.e. no missing extant species), the method can now use incomplete phylogenies where either all taxa are included but in unresolved clades ('terminally unresolved' approach) or where only a subset assumed to be randomly sampled are included ('skeleton tree' approach) (FitzJohn *et al.*, 2009). Building on this framework, a variety of related models have been developed to examine other scenarios, such as quantitative trait evolution (QuaSSE; FitzJohn, 2010), interactions of multiple traits (MuSSE; FitzJohn, 2012) and cladogenetic trait evolution (ClaSSE: Goldberg & Igic, 2012; BiSSE-ness: Magnuson-Ford & Otto, 2012) (Fig. 2). By comparing different constraints on the full models, biologists can test a wide range of evolutionary hypotheses, such as directional trends and evolutionary dead ends (Table 1). The resulting best fitting model can also be used for ancestral state reconstruction (see Goldberg *et al.*, 2008). Although the application of these new methods relieves the need to reconstruct ancestral states prior to conducting tests of SDD, these methods may, however, be susceptible to false positives when the trait of interest only evolved once, or rarely, on the tree (Maddison & FitzJohn, *in press*).

The development of these new parametric SDD methods has resulted in renewed interest in the evolution of traits previously hypothesized to shape patterns of diversification (Jablonski, 2008 and references therein). Because of the problems associated with earlier studies using sister group comparisons, the application of new SDD models has the potential to overturn classic examples of SDD. In the following sections, we review the findings from recent work, focusing on evolutionary dead ends, key innovations and geographic traits.

Traits that affect diversification

Evolutionary dead ends

Evolutionary dead ends are traits that increase the likelihood of extinction, but become fixed within species because they are thought to initially provide a short-term evolutionary advantage (Stebbins, 1957; Schwander & Crespi, 2009; Wright *et al.*, 2013). Some classic hypothesized dead ends include asexuality (Maynard Smith, 1978; Lynch *et al.*, 1993), selfing (Stebbins, 1957; Takebayashi & Morrell, 2001; Wright *et al.*, 2013), polyploidy (Stebbins, 1957) and specialization (Cope, 1896; Simpson, 1944; Mayr, 1963; Moran, 1988). The increased extinction rate associated with evolutionary dead ends is predicted to result in a 'tippy' or 'twiggy' phylogenetic pattern whereby the species with these traits appear widely dispersed across the tips of phylogenetic trees (Kelley & Farrell, 1998; Schwander & Crespi, 2009). The ability to revert to the ancestral state would alleviate the disadvantages of evolutionary dead ends, and therefore, such traits are

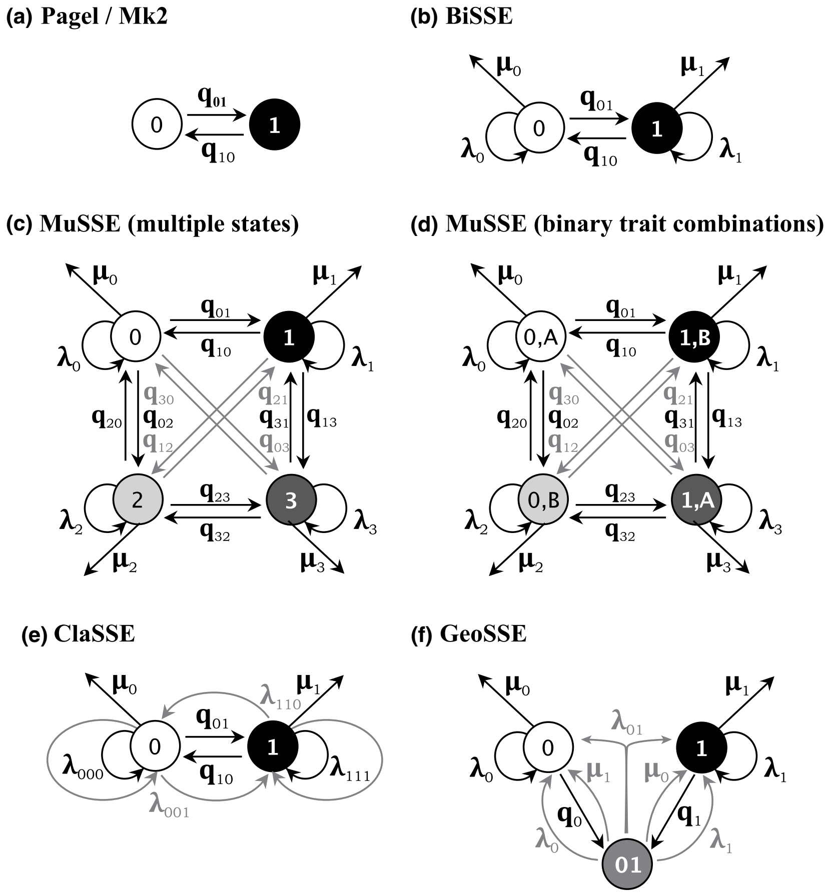
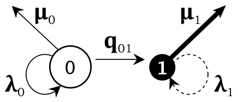
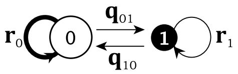
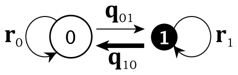
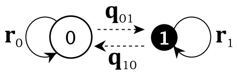
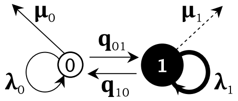
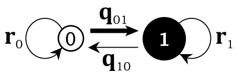


Fig. 2 Model parameters for state-independent and dependent diversification models. Character states are represented by numbers in circles. For each state, the models estimate speciation (λ), extinction (μ) and transition rates (q), with the respective character state shown in subscript. Two character states are shown in subscript following q to represent the transition rate from one character state to the other (first and second numbers, respectively). Different shaded arrows are for clarity. (a) Pagel's transition rate framework (also known as the Mk2 model) represents a state-independent model whereby speciation and extinction rates for each character state (not shown) are assumed to be equal. (b–f) Models that allow for state-dependent diversification: (b) BiSSE and (c–f) extensions of BiSSE. (b) BiSSE in its original formulation for binary states with six rate parameters. (c) MuSSE allows SDD analyses for more than two character states as well as (d) combinations of two or more binary traits. Note that this two character model is analogous to Pagel's dependent model used for his omnibus test of correlated evolution (Pagel, 1994). (e) ClaSSE adds additional rate parameters to test for character change that occurs at a speciation event. Subscript following λ describes the state of the parent followed by the state of each daughter lineage. Speciation rates that involve both daughter lineages assuming a new state (λ_{011}, λ_{100}) are not shown. BiSSE-ness, a method that similarly includes the possibility of cladogenetic trait evolution, is not depicted. (f) GeoSSE focuses on geographic characters where taxa with state 0 inhabit a different geographical area to taxa with state 1. Taxa with state 01 inhabit both geographical areas. GeoSSE estimates an additional parameter (λ_{01}) in addition to the same rate parameters as BiSSE to accommodate that speciation can occur between regions.

also not thought to be able to transition back to the ancestral state (Takebayashi & Morrell, 2001; Igic & Busch, 2013).

Recent studies suggest that although some classic evolutionary dead ends fit this dual requirement of irreversibility and increased extinction, many 'tippy' distributions arise due to other evolutionary processes (Table 1). For example, the relative rarity of white-flowered species in morning glories is best explained by differences in diversification rates with no evidence of irreversible pigment loss (as in Table 1 A2) (Smith *et al.*, 2010). In a particularly surprising case, Johnson *et al.* (2011) found that, despite their twiggy distribution, asexual lineages of primrose actually diversify over eight times faster than sexual lineages. Their paucity relative to sexual lineages is instead due to high rates of reversions back to sexual reproduction (as in Table 1 A3). By contrast, even though extinction rates are notoriously difficult to estimate (Maddison *et al.*, 2007; Quental & Marshall, 2010; Rabosky, 2010; Davis *et al.*, 2013), both polypoidy and self-compatibility in plants appear to fit the criteria of an evolutionary dead end,

Table 1 Alternative hypotheses that can be tested using BiSSE to explain disparities in clade size associated with binary traits. BiSSE simultaneously estimates rate parameters for the ancestral and derived state (0 and 1, respectively, represented as circles), each of which can be constrained for hypothesis testing: speciation (λ_0, λ_1), extinction (μ_0, μ_1) and transition rates (q_{01}, q_{10}). Diversification rates ($r_{0 \text{ or } 1}$) can be calculated as $r_0 = \lambda_0 - \mu_0$ and $r_1 = \lambda_1 - \mu_1$. Different hypotheses can be tested for statistical significance using either a maximum-likelihood framework, with likelihood ratio tests for nested models or Akaike information criterion, or a Bayesian framework by comparing credibility intervals from a Markov chain Monte Carlo sample of parameter values. Larger circles (for 0 or 1) indicate the state that is found in a higher proportion of extant taxa. Thicker arrows indicate higher parameter values (rates) whereas dotted arrows represent lower values. Note that these processes are not necessarily mutually exclusive.

Process	Expectation	Schematic of expectation
Higher proportion of taxa with ancestral character state		
(A1) *Evolutionary dead end*: Increased extinction rates associated with state 1 and irreversible character evolution	$\lambda_0 = \lambda_1$ or $\lambda_0 > \lambda_1$ $\mu_0 < \mu_1$ $q_{10} = 0$	
(A2) *Asymmetrical diversification*: Higher diversification rates in the ancestral state	$r_0 > r_1$ $q_{01} = q_{10}$	
(A3) *Asymmetrical transitions (directional evolution)*: Higher rate of character loss than gain	$r_0 = r_1$ $q_{01} < q_{10}$	
(A4) *Nonequilibrium dynamics*: Low transition from the ancestral state to the derived state	$r_0 = r_1$ $q_{01} = q_{10} \sim 0$	
Higher proportion of taxa with derived character state		
(B1) *Key innovation*: Increased diversification of species with state 1	$\lambda_0 < \lambda_1$ $\mu_0 = \mu_1$ or $\mu_0 > \mu_1$ $q_{01} = q_{10}$	
(B2) *Asymmetrical transitions (directional evolution)*: Higher rate of character gain than loss	$r_0 = r_1$ $q_{01} > q_{10}$	

whereby lineages with these states experience higher extinction rates, and transitions from the ancestral state to these derived state are irreversible (as in Table 1 A1) (Goldberg *et al.*, 2010; Mayrose *et al.*, 2011). Consistent with the idea that dead end traits could be fixed due to short-term advantages, Goldberg *et al.* (2010) also found that self-compatible lineages had a higher speciation rate but, given their high extinction rate, they had an overall lower diversification rate. Both of these cases were supported by independent information suggesting that reversals were highly unlikely. Collectively, these studies suggest that true evolutionary dead ends, which both increase the likelihood of extinction and are irreversible, may be much rarer than previously hypothesized.

Key innovations

The term 'key innovation' is perhaps one of the most widely but inconsistently applied terms in evolutionary biology (Hunter, 1998; Galis, 2001). Some have defined key innovations as novel features that permit lineages to exploit new habitats or resources (Simpson, 1953; Mayr, 1963; Van Valen, 1971; Baum & Larson, 1991), whereas others consider key innovations to be traits that trigger species diversification (Erwin 1992; Heard and Hauser 1995). Of course, these two elements may be directly linked: the evolution of trait novelty may allow lineages to access new ecological opportunities and lead to diversification through the process of adaptive radiation (Schluter, 2000; Glor, 2010; Yoder *et al.*, 2010). Work in phylogenetic comparative methods has focused on the diversification aspect of key innovations, aiming to identify features that increase the rate of lineage diversification, either by increasing speciation rates or by decreasing extinction rates.

One challenge in the study of key innovations has been that many purported examples, such as the angiosperm flower or the vertebrate jaw, appear to have evolved a single time. In this case, it is impossible to test whether that character, or another synapomorphy of the same clade, is tied to the proliferation of species (Galis, 2001; Ree *et al.*, 2005; Maddison & FitzJohn, *in press*). Thus, the best support for key innovations comes from cases where the trait has arisen multiple times, making it possible to ask whether independent origins of the trait consistently lead to increased diversification (Mitter *et al.*, 1988; Hodges & Arnold, 1995; de Queiroz, 2002). Although convergent evolution of key innovations mitigates the synapomorphy problem, it does not eliminate the possibility that other evolutionary processes, such as directional trends, can produce a similar abundance of taxa with the derived state (Table 1B). Thus, studies that jointly estimate the transition rates and diversification rates have the potential to alter our views on key innovations previously identified using sister group comparisons.

Applications of new SDD models to test key innovations suggest that although a wide range of characters can act to increase diversification rates (through both differential speciation and differential extinction), biased transition rates often contribute to patterns of phenotypic diversity. For example, achenes (single-seeded dry fruits) are particularly common in the campanulid angiosperms, and this pattern is due to both higher diversification rates of species with achenes and directional evolution, whereby gains of achenes are more likely than losses (Beaulieu & Donoghue, 2013). Other studies have found similar combinations of biased transition rates and differential diversification (e.g. Lynch, 2009; Maia *et al.*, 2013; Hernández-Hernández *et al.*, 2014) and, in some cases, were able to distinguish increased speciation from decreased extinction as the mechanism driving differential diversification. For example, both CAM metabolism and the tank habit, an external water and nutrient reservoir, appear to be key innovations in bromeliads, but the evolution of CAM acts by increasing speciation rates, possibly facilitating invasion of dry habitats, whereas the tank habit decreases extinction rates (Silvestro *et al.*, 2014). Nonetheless, some authors have found no effect of major functional innovations, such as adhesive toepads in geckos, on diversification (Gamble *et al.*, 2012). However, this study, which also did not find evidence of directional transitions, opens the door to testing whether other traits, such as nocturnality and dietary shifts, may explain the incredible species richness of geckos relative to other lizard groups.

A surprisingly small number of studies thus far have shown patterns of phenotypic diversity to be solely due to differential diversification without any influence from biased transitions (e.g. tank habit; Silvestro *et al.*, 2014). Rather, these studies have shown that directional transitions play an equal, or in some cases, greater role in increasing the abundance of taxa with particular traits. Nonetheless, many classic key innovations from across the tree of life, from nectar spurs in flowers to venom in snakes, have yet to be examined with joint estimation SDD models, leaving more to be learned about the types of traits that increase diversification and the ways in which they do so.

Geographic range

Like morphology, life history, and many other traits, geographic distribution is a heritable feature that can affect the rate at which lineages diversify (Jablonski, 1987). For example, the immense species richness in biodiversity hotspots has often been linked with higher speciation rates and/or lower extinction rates in those areas (Latimer *et al.*, 2005; Sauquet *et al.*, 2009; Lancaster & Kay, 2013). However, other processes, such as directional trends in dispersal, can also lead to differences in species richness across geographic areas (Gaston, 1998), analogous to the way in which asymmetrical transition rates can produce patterns similar to differential diversification. For instance, a recent study suggests that a high frequency of latitudinal zone switching, rather than differential diversification in tropical vs. temperate zones, may underlie latitudinal diversity patterns (Jansson *et al.*, 2013). Despite parallels with the comparative approaches for studying morphotypic characters, geographic traits possess unique features that have led to the development of a separate set of models (Ree *et al.*, 2005; Goldberg *et al.*, 2011). First, character states for geographic traits are often nonindependent, where states for widespread taxa may be composites of other states (e.g. inhabitance of both North and South America). Second, changes in state may directly coincide with extinction and speciation events. Following the previous example, extinction of the widespread taxon in one part of its range (say, North America) would convert its state to South America. Also, state changes for geographic characters are often expected to occur during speciation (cladogenesis) if, for example, lineage-splitting coincides with a dispersal or vicariance event. Models that account for these complex interactions between range evolution, speciation and extinction quickly become parameter-rich, limiting the number of geographic areas that can be considered. This, along with the fact that these methods became available only recently, may explain why only a few studies have implemented SDD models for range evolution (e.g. Valente *et al.*, 2010; Cardillo & Pratt, 2013). However, even with a limited number of regions (Fig. 2f; see also Goldberg & Igic [2012] as a way to increase the number of areas), these methods have the potential to provide new insight about fundamental biogeographic questions, such as the importance of source-sink dynamics in shaping species distributions (Goldberg *et al.*, 2011) and the effects of range size on speciation and extinction rates (Darwin, 1859; Mayr, 1963; Rosenzweig, 1995; Gaston, 2003).

Are there traits that do not affect diversification?

Given the wide range of traits that have been implicated in affecting diversification (Jablonski, 2008; Dynesius & Jansson, 2014), it is reasonable to ask whether there are any traits for which models that ignore SDD would be appropriate. Traits that influence the temporal persistence of new species are thought to affect macroevolutionary diversification (Allmon, 1992; Ricklefs & Bermingham, 2007; Rosenblum *et al.*, 2012; Dynesius & Jansson, 2014), and likely act (directly or indirectly) by altering patterns of gene flow, for example, by increasing dispersal ability or allowing the successful invasion of new niche space. Thus, traits that *a priori* are not expected to alter gene flow, such as defensive traits, may be the least likely candidates for an effect on diversification. However, it is possible that with the evolution of particular morphological or behavioural traits, sexual selection may evolve (e.g. body size differences due to different predator regimes; Langerhans *et al.*, 2007; Head *et al.*, 2013), leading to premating reproductive isolation and potentially, speciation. Likewise, if particular traits are tightly linked with interactions with other species, they may co-evolve with the associated species to drive diversification (e.g. plant defence traits and herbivores; Ehrlich & Raven, 1964; Agrawal *et al.*, 2009). Given these considerations, models allowing for SDD will often be the most conservative approach, even when the goal of analysis is not to test for differential diversification *per se* (e.g. ancestral state reconstruction or tests of correlated evolution). Nonetheless, the addition of diversification parameters requires greater power in the data set, and the exact size of the data set needed depends on the structure of the data (e.g. the distribution of character states, the shape of the tree). Simulation approaches, Monte Carlo-based methods, and predictive approximate Bayesian computation (ABC) techniques provide multiple avenues for estimating power and accuracy as part of implementing these comparative methods (Boettiger *et al.*, 2012; Davis *et al.*, 2013; Brown, 2014).

Conclusions

Similar to the way in which independent contrasts (Felsenstein, 1985) paved the way for major progress in comparative methods for quantitative traits (e.g. PGLS; Grafen, 1989; Blomberg's K; Blomberg *et al.*, 2003; DOT test; Ackerly *et al.*, 2006), the publication of joint character evolution and diversification rates models (Maddison *et al.*, 2007) has triggered the development of an entire suite of methods applicable to a broader range of traits and evolutionary questions (e.g. FitzJohn, 2010; Goldberg *et al.*, 2011; Magnuson-Ford & Otto, 2012). The use of these methods has exposed some of the complexities of testing SDD, such as the potential for transition rate asymmetries to produce patterns similar to key innovations and dead ends (e.g. Johnson *et al.*, 2011). Although differences in rates of gain and loss are biologically realistic for many traits (Ree & Donoghue, 1999; Wiens, 2001), distinguishing these trends from differential diversification was previously difficult in the absence of joint models (Maddison, 2006).

With these new and potentially powerful methods, however, modern comparative biologists find themselves faced with a fresh set of challenges. As the range of comparative methods continues to expand, there are a myriad of options for building complex evolutionary models for continuous or discrete characters, with a single or multiple characters, with anagenetic and/or cladogenetic trait changes, etc. It is also possible to allow for heterogeneity in processes (e.g. transition rates) across the tree or over time (e.g. Johnson *et al.*, 2011), although there is no well-developed approach for simultaneously identifying the optimal number and placement of break points (as in Alfaro *et al.*, 2009). With this flexibility, it is tempting to saturate analyses with parameters to capture the range of biological phenomena that may play a part in a lineage's history. However, creating empirical data sets with the hundreds of species needed for evaluating complex models may be arduous (especially as the most interesting characters are often time-consuming to score) and, in some cases, this effort may be unnecessary if the same questions can be adequately addressed with simpler models. Thus, we stress the need for careful experimental design that considers the match between the macroevolutionary questions, the study system, and the available methods (Freckleton, 2009). As with any experiment, comparative biologists should take the time to explore their data and consider alternative explanations (such as a codistributed character) in interpreting significant results from diversification analyses (Maddison *et al.*, 2007; Maddison & FitzJohn, *in press*).

In the coming years, we anticipate continued development to extend existing phylogenetic comparative methods to include diversification parameters and to create new bridges with palaeontological research. For example, in the same way that the MuSSE model allows for SDD to be included in Pagel's (1994) test of correlated evolution, the QuaSSE model for continuous traits could be extended to create the equivalent of phylogenetic generalized least squares (Grafen, 1989) for estimating trait correlations. An SDD extension of phylogenetic path analysis (Hardenberg & Gonzalez-Voyer, 2013) would also be appealing for cases where a researcher predicts that a character affects diversification, but only indirectly through its effects on another character. There is also great interest in integrating fossil information with data from extant taxa (Fritz *et al.*, 2013; Pennell & Harmon, 2013), which will also help increase the power to estimate extinction rates (Quental & Marshall, 2010; Rabosky, 2010; Pyron & Burbrink, 2012); however, much of this effort has thus far only focused on character evolution (e.g. Slater *et al.*, 2012) rather than the joint estimation of transition and diversification rates. Furthermore, there has also been increasing focus on the effect of species interactions and changing abiotic and biotic conditions on patterns of diversity (reviewed in Pyron & Burbrink, 2013;

Rabosky, 2013; Morlon, 2014). The integration of SDD, diversity dependent rates and rate heterogeneity throughout the tree in the same analysis is still yet to come.

As these statistical comparative analyses bring greater insight into the types of traits that shape lineage history, a grand challenge is to connect results about macroevolutionary processes with processes observed at an ecological timescale (e.g. Kisel *et al.*, 2012; Rabosky & Matute, 2013). Comparative approaches provide powerful tools for testing evolutionary questions at broad scales, such as whether trait evolution exhibits directional trends or whether functional innovations are required for adaptive radiations. However, understanding the biology that underlies such findings relies on integrating knowledge and approaches from other fields. For example, directional evolution may arise due to the nature of the genetic or developmental changes associated with phenotypic transitions (Igic *et al.*, 2006; Rausher, 2008). Determining the mechanisms by which traits alter diversification rates may be even more challenging. For key innovations, a reasonable first step may be to functionally test how the trait changes ecological performance (Galis, 2001), whereas for evolutionary dead ends, experiments may target whether the trait limits adaptive evolution. Ultimately, integrating phylogenetic comparative methods with other approaches, from development to ecology, will provide a more comprehensive understanding of the proximate causes of SDD. Together, this combined approach studying both macro- and microevolutionary processes will allow us to get to the root of how traits shape trees.

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