

Evolutionary Bangs and Whimpers: Methodological Advances and Conceptual Frameworks for Studying Exceptional Diversification

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Even a casual glance at the pages of Systematic Biology today will reveal that phylogenetic biology is about much more than the reconstruction of evolutionary relationships among species. Phylogenies are everywhere in evolutionary biology and—increasingly—in fields ranging from community ecology (Cavender-Bares et al. 2009) to cultural anthropology (Gray et al. 2009). Phylogenies contain information about both the pattern and timing of speciation events within clades, and there has been great interest in leveraging this information toward fundamental questions in macroevolution. Why do some clades—or geographic regions—have more species than others? What regulates species diversity through time? Do different traits or character states have predictable effects on speciation and extinction? Are processes that govern the distribution of species richness across the Tree of Life scale dependent, such that patterns in species-level phylogenies are qualitatively distinct from patterns at higher taxonomic levels? Do general rules characterize patterns of speciation and extinction during adaptive radiation?

Fueled by a rapid increase in the availability of time-calibrated molecular phylogenies and new comparative methods for analyzing diversification, the number of studies dealing with rates and patterns of species diversification has exploded in recent years. Recent syntheses, for example, have explored diversification patterns in hundreds of species-level molecular phylogenies (McPeck 2008; Phillimore and Price 2008; Venditti et al. 2010) and across large higher-level phylogenies that contain information on thousands of taxa (Bininda-Emonds et al. 2007; Alfaro et al. 2009). To what extent has the increase in data availability for diversification studies clarified the underlying evolutionary processes that generated those data? Many important methodological advances have been made since the Society of Systematic Biologists' 2001 Symposium on the use of phylogenetic tree shape metrics in the study of evolution (Mooers and Heard 2002), but there is perhaps a decreasing consensus on how to interpret many widely used approaches. Three examples from the recent literature illustrate this point.

Diversification “Slowdowns”

The gamma statistic (Pybus and Harvey 2000), a metric of the distribution of speciation times in molecular phylogenies, remains one of the most commonly

used methods to test for evidence of adaptive radiation. Negative values of gamma are assumed to represent slowdowns in the rate of speciation through time, and empirical studies suggest that clades with negative gamma values are widely distributed across the tree of life (McPeck 2008; Phillimore and Price 2008). These apparent “bursts” of lineage accumulation early in the history of evolutionary radiations suggest strong ecological controls on speciation, with consequent declines in diversification rates as diversity rises and ecological niches are filled. Yet, recent work demonstrates that apparent slowdowns in clade diversification can be produced by a range of alternative processes (Quental and Marshall 2010), including those where net diversification rates have not changed at all through time (Rabosky 2009b). These theoretical considerations are compounded by evidence that artifacts of taxon sampling and phylogeny reconstruction can lead to biased inferences about rates of species diversification through time (Revell et al. 2005; Cusimano and Renner 2010). The extent to which lineage accumulation patterns in empirical phylogenies reflect a predominant role for adaptive radiation remains unclear.

Character States and Diversification Rates

Key traits are often invoked to explain patterns of differential diversification (Mitter et al. 1988; Heard and Hauser 1995). However, Maddison and colleagues (Maddison 2006; Maddison et al. 2007; FitzJohn et al. 2009) have demonstrated that inferences about character evolution and diversification cannot necessarily be made independently. If character states are associated with different rates of speciation and/or extinction, then inferences about rates of character evolution may be biased; likewise, asymmetric rates of character change can lead to biased estimates of diversification rates. This observation has broad implications for comparative biology because it implies that studying processes of either character evolution or diversification may require simultaneous analysis of both (Maddison et al. 2007).

Extinction and Molecular Phylogenies

In principle, it is possible to estimate extinction rates from molecular phylogenies of living taxa only (Nee et al. 1994). However, recent studies have challenged

what we can infer about extinction in the absence of data from the fossil record (Rabosky 2009b; Quental and Marshall 2010; Rabosky 2010a). The widespread observation of extremely low extinction rates in molecular phylogenies (Purvis 2008) is in direct conflict with the fossil record, which suggests that evolutionary radiations frequently occur against a background of high extinction (Alroy 2008; Quental and Marshall 2010).

These examples highlight several challenging issues in diversification studies and further hint at the rapid expansion of research in this area during the past 5 years. The accelerated pace of theoretical and methodological work in this area motivated us to organize a symposium dedicated to conceptual and methodological issues in the study of species diversification, held at the 2009 meeting of the Society of Systematic Biologists in Moscow, Idaho. Our principal objective was to bring researchers together to discuss emerging methodologies and new conceptual frameworks for data interpretation.

THE SYMPOSIUM

Seven researchers presented original work at the symposium. Collectively, their results painted a picture of a discipline in transition: Exciting new statistical approaches for studying diversification were balanced with novel interpretations of phylogenetic diversity patterns. The four papers assembled for this volume represent an intriguing cross section of both the symposium as well as current issues in macroevolution as seen through the lens of molecular phylogenies.

The paper by FitzJohn (2010) is the latest in an influential series of papers (Maddison et al. 2007; FitzJohn et al. 2009) that have broadened the scope of “diversification rates” to include the process of character change itself through the recognition that inferences about rates of character change and diversification cannot be made independently. Previous work has explored state-dependent speciation extinction (SSE) models for binary characters (BiSSE; Maddison et al. 2007). Here, FitzJohn (2010) extends this model to quantitative characters (QuaSSE), using a diffusion model for character change and arbitrary linking functions between character states and speciation/extinction rates. This is an exciting methodological development that will enable researchers to conduct rigorous tests of the association between traits like body size and diversification rates.

Time-calibrated phylogenetic trees for higher taxa are frequently used in the analysis of diversification rates because they contain information about both the ages of constituent clades as well as their species richness. Diversification rates are often estimated for clades under the assumption that rates are constant through time. The paper by Rabosky (2010b) argues that species richness within clades can be a function of very different processes and that some of these processes are fundamentally incompatible with estimators of net diversification rates that assume rate constancy through time. Rabosky (2010b) explores the properties of a simple model where

clade diversity is a function of total time-integrated speciation (Ω), and where species richness for all clades is drawn from the same distribution regardless of clade age. His results suggest that the Ω model provides a better explanation for diversity patterns than constant-rate birth–death models when there is no relationship between the ages of clades and their species richness, a pattern that appears to characterize many empirical data sets (Ricklefs 2007; Rabosky 2009a). This is consistent with the hypothesis that clade diversity may be regulated by diversity dependence of speciation and/or extinction rates (Ricklefs 2007) and suggests that for many data sets, it may not even be possible to estimate diversification rates.

If species diversity is regulated by equilibrium processes, such as diversity-dependent speciation and extinction rates, what signal would such processes be expected to leave in species-level molecular phylogenies? This is the focus of the paper by Liow et al. (2010), who generate complete species level phylogenies under various scenarios of diversity dependence. Their results demonstrate that a range of diversification processes can leave indistinguishable patterns in molecular phylogenies, including exponential clade growth and species turnover at constant diversity. By simulating both “fossil records” and molecular phylogenies simultaneously, Liow et al. (2010) are able to contrast the ability of phylogenetic and paleontological data to recover both diversity dynamics and diversification rates. They find much greater power to recover “true” evolutionary scenarios when information from the fossil record is included, particularly under an equilibrium model of diversity regulation with stochastically constant diversity through time. Their results argue strongly for better integration of molecular phylogenetic and fossil data in diversification studies.

Our expectations for exceptional versus unexceptional patterns of diversification have been in large part shaped by pure birth (Yule 1924) and birth–death (Kendall 1948) models. These models, which are ubiquitous in macroevolutionary studies (Nee 2006), explain phylogenies as the outcome of a branching process where each lineage has a probability of speciation or extinction. Although these models have played an important role in macroevolutionary studies, they ignore geography, which is likely to be a fundamental component of cladogenesis in any species where changes to geographic range size influence probabilities of speciation and extinction. Pigot et al. (2010) develop a neutral model of geographic diversification and use simulations to explore how geographic parameters influence the tree shape and the timing of branching events. They find that trees produced under a geographic model can differ from birth–death expectations in being either more balanced or more imbalanced, depending on the relative importance of vicariance and dispersal to speciation. They also find that slowdowns in diversification rate, which are often interpreted as evidence for ecological niche filling, arise under a geographic model simply as an outcome

of range size reduction in daughter species following allopatric speciation. Their results illustrate how our inferences of evolutionary process are strongly dependent on the models and highlight as well the need for a greater consideration of clade geographic dynamics in macroevolutionary studies.

Three symposium presenters whose work is not published in this volume include Michael Alfaro, Brian Moore, and Mark McPeck. Alfaro's talk focused on broad-scale patterns of diversification across the vertebrate tree of life (Alfaro et al. 2009) as well as methods for inferring rates of speciation and extinction by integrating molecular phylogenies with paleontological data. Moore presented new Bayesian methods for inferring variation in diversification rates across phylogenetic trees. Finally, McPeck discussed an ecological metacommunity model that could potentially explain many patterns of lineage accumulation in species-level molecular phylogenies.

Prospects for the Future

The papers presented at this symposium, in conjunction with recent developments in the literature, sound a cautionary note regarding the interpretation of diversification patterns from molecular phylogenies. Yet molecular phylogenies provide a critical window into the history of life that can potentially enable us to address some of the most fundamental questions in evolutionary biology. Although the limitations of simple models are increasingly apparent, we are gaining insights into diversification processes through the use of more sophisticated approaches as illustrated by the geographic (Pigot et al. 2010), Ω (Rabosky 2010b), and QuaSSE (FitzJohn 2010) models presented here. However, molecular phylogenies considered alone will always be inadequate on some level: There is simply a limited amount of information contained within even fully resolved time-calibrated trees (e.g., Liow et al. 2010).

Integrating phylogenies with other types of data will be a major avenue for future progress in the field of macroevolution. One key frontier is the divide between molecular phylogenetic and fossil-based diversification studies. Researchers in both areas are keenly interested in the dynamics of origination, extinction, and diversity across the tree of life, but the lack of integration between paleontological and neontological data is startling. Many challenges exist to the development of analytical frameworks that can incorporate both the stratigraphic record and molecular phylogenies, and identifying appropriate empirical data sets may prove equally difficult. However, such integration is needed to reconcile the discord between diversification patterns in the fossil record and molecular phylogenies (e.g., Bininda-Emonds et al. 2007; Quental and Marshall 2010) and will provide a much better understanding of the factors that control the fates of clades through time. Robust tests of processes (e.g., adaptive radiation,

ecological limits on clade size, and species selection) will require new approaches that combine molecular phylogenies with other kinds of data as well, such as geographic, ecological, and phenotypic characters. The simultaneous study of character evolution and diversification rates (Maddison et al. 2007; FitzJohn 2010) is an especially promising approach, and landscape of possibilities for this class of models has scarcely been explored. Likewise, integrating phylogenies with ecological community dynamics may provide new insights into the ecological basis of speciation and extinction (Mooers et al. 2007; McPeck 2008).

As suggested by the papers presented in this volume, we are a long way from "black box" solutions in diversification analyses, and the rapid turnover of ideas and methods implies that care is needed in the interpretation of empirical patterns. To us, this indicates that the study of diversification rates from phylogenetic data is a conceptually rich field with tremendous room for theoretical and methodological innovation.

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