# REVIEW ARTICLE

# Radiation and extinction: investigating clade dynamics in deep time

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The field of macroevolutionary research has grown rapidly in recent decades, bringing new sources of data and rigorous new methodologies to the analysis of organismal evolution through deep time. In November 2014, a 2-day symposium and workshop on 'Radiations and Extinctions: Clade Dynamics in Deep Time' was held at the Linnean Society of London and Imperial College London, with the goal of bringing together a diverse array of researchers developing and applying methods for reconstructing deep-time macroevolutionary patterns in biodiversity, with a particular focus on analytical approaches that take advantage of the wealth of data available in the fossil record. In this special issue, contributors to this meeting present and critique methodologies for examining radiations, extinctions, and clade dynamics through deep time and apply these approaches to a range of taxonomic groups, time intervals, and themes, including speciation and extinction, ecometric patterning, evolutionary rates, and morphological disparity. Combined, this special issue covers topics that are fundamental to macroevolutionary research and provides a valuable resource on cutting-edge analytical approaches in this field. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **118**, 6–12.

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## INTRODUCTION

Determining the causes and drivers of evolutionary dynamics is central to our understanding of life on Earth. What factors shaped the modern biota? Why did some groups go extinct, whereas others survived and radiated? Why are some groups so much more diverse than others? What will happen to organisms as the Earth continues to warm up? Many of these questions have inspired scientists for centuries (Cuvier, 1825; Darwin, 1859; Simpson, 1944), with foundational work in developmental biology, comparative anatomy, palaeontology, and geology providing provocative hypotheses that still influence current research on organismal evolution. New sources of data, however, from recent advances in molecular biology, computing, and imaging, as well as increasingly sophisticated quantitative methods, have provided an unprecedented ability to test these hypotheses rigorously.

George Gaylord Simpson (1944) set the groundwork for the application of statistics to macroevolution, and he championed the seamless transition from modern to fossil samples in exploring these themes, although he could not have foreseen the remarkable advances over the subsequent 70 years. Simpson was passionate about systematics, and yet he could not then have conceived of the revolution wrought by the application of cladistics and phylogenomics to the generation of huge phylogenetic

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trees (Bininda-Emonds, Gittleman & Purvis, 1999; Wiens *et al.*, 2010; Meredith *et al.*, 2011; Jetz *et al.*, 2012; dos Reis *et al.*, 2012). He was also knowledgeable about stratigraphy but, equally, he could not have imagined the orders-of-magnitude improvements to the dating of the rock record and consequent refinements to the calibration and dating of time trees that then permit meaningful calculations of rates of evolution across trees (Yang & Rannala, 2006; Donoghue & Benton, 2007; Aze *et al.*, 2011; Brown & Yang, 2011; Stadler, 2011). Finally, he could not have imagined how advances in computing capacity and in numerical methods and algorithms, as well as the creation of massive multi-contributor databases (e.g. The Paleobiology Database; www.paleobiodb.org), would have brought powerful multivariate and iterative approaches to bear on the problems he felt were closest to his heart (Jablonski & Chaloner, 1994; Alroy, 1999; Jablonski, 2001; Alfaro *et al.*, 2009; Harmon *et al.*, 2010; Losos, 2010; Hunt, 2012). Despite some wobbles in the 1980s and 1990s, it is surely right that phylogenomicists and palaeontologists now share problems, data, and solutions. The result has been an explosion of studies in recent years (Fig. 1) reconstructing rates and patterns of evolution, testing complex evolutionary models, and examining the effects of intrinsic and extrinsic drivers on biodiversity, with palaeontological, neontological, and genomic data sets. These studies demonstrate the importance of examining evolution across deep time scales, incorporating extinct taxa and encompassing many previous shifts in climate 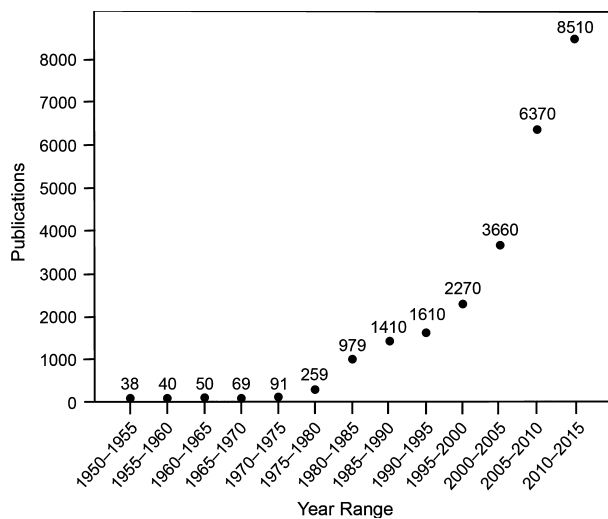and environment, including those potentially analogous to the modern world (Bown, Holroyd & Rose, 1994; Jablonski, 2001; Zachos *et al.*, 2001; Hunt, 2007; Slater, Harmon & Alfaro, 2012; Finarelli & Goswami, 2013). Only by taking full advantage of the rich data available for past and present biotas can we hope to understand the processes that generate and shape organismal diversity.

In November 2014, a 2-day symposium and workshop on 'Radiations and Extinctions: Clade Dynamics in Deep Time' was held at the Linnean Society of London and Imperial College London, with the goal of bringing together a diverse array of researchers developing and applying methods for reconstructing deep-time macroevolutionary patterns in biodiversity, with a particular focus on analytical approaches that take advantage of the wealth of data available in the fossil record. Speakers detailed both methodology and application for a range of taxonomic groups, time intervals, and macroevolutionary themes corresponding to radiation, extinction, and clade dynamics in deep time. The first day of presentations and discussions was followed by a second day of workshops in which participants were shown how to apply these new methodologies to their own datasets. In this special issue, many of the contributors to this meeting present detailed descriptions of new methods, conduct critical reviews and analyses of existing approaches, and apply these approaches to fundamental questions on the evolution of the modern biota.

## SPECIATION AND TAXONOMIC DIVERSITY

Taxonomic diversity has been a cornerstone of macroevolutionary and macroecological research for decades, with highlights including groundbreaking work by Raup & Sepkoski, (1982) on marine invertebrate diversity, which identified five mass extinctions in the Phanerozoic Eon and inspired a generation of researchers to investigate the validity, causes, and effects of these phenomena across diverse clades (e.g. see the study by Halliday & Goswami, 2016 in this special issue on the effects of the Cretaceous/Palaeogene mass extinction on mammal disparity). Taxonomic diversity is the product of the generation of new species and the loss of existing species, and isolating these attributes and understanding the factors that cause variations in them is fundamental to reconstructing the evolution of diversity. In this special issue, Rabosky (2016) examines the causes of variation in rates of speciation. In generating biodiversity, the balance between speciation and extinction is key, and high rates of speciation characterize many so-called 'explosive' radiations, such as cichlid fishes or Palaeogene mammals. In particular, he



**Figure 1.** Publications relating to macroevolution, binned in 5-year intervals, as identified by Google Scholar using the search term 'macroevolution' on 1 December 2015.

discusses why speciation rates are so variable across the tree of life, with sister clades often exhibiting hugely different modern diversities (e.g. compare monotremes and therian mammals, or holostean and teleost fishes, or crocodylians and birds). He points out that perhaps too much research has focused on reproductive isolation, and all the barriers to gene pool mixing that emerge during the process of species formation, to the exclusion of other determinants of speciation rate. In cases of closely-related clades that differ in diversity by orders of magnitude, as just noted, it is likely that they all had the same original modes of reproductive isolation, such that other factors must have determined their subsequent massively different evolutionary trajectories. These other factors include the innate rate of splitting within a clade, as well as population persistence in which incipient species avoid demographic extinction.

Finarelli & Liow (2016) continue on the theme of taxonomic diversification with a detailed study of the past 28 Myr of northern hemisphere carnivoran mammal diversification, using an extensive dataset of fossil occurrences extracted from The Paleobiology Database. They borrow from sampling strategies utilized in ecological research, applying a capture–mark–recapture approach to ameliorate biases in our sampling of the fossil record. Although their total dataset ('global') analysis recovered a relatively stable net diversification, their results demonstrate geographical variation, especially in the late Neogene. A peak in positive diversification is restricted to Eurasia 9–8 Mya, and coincides with large-scale vegetation changes that dramatically altered the regional climate. Similar vegetational changes in North America did not occur until a few million years later. By contrast, 6–5 Mya, North American carnivorans showed a positive diversification peak, whereas their Eurasian counterparts suffered negative diversification, coinciding with the Messinian Salinity Crisis. With the exception of Caniformia (the group that includes dogs and bears), which has lower speciation rates in North America than in Europe, net rates of diversification do not differ between other carnivoran subclades, nor between the two regions. The study by Finarelli & Liow (2016) adds to the growing body of literature demonstrating the importance of examining regional, as well as global, patterns of palaeodiversity (Jackson & Johnson, 2001; Vermeij & Leighton, 2003; Mannion *et al.*, 2015).

## MODELLING TRAIT EVOLUTION

Clades not only evolve in numbers, but also in form, and macroevolutionary analyses of the evolution of traits have benefited greatly from developments in image data collection, morphometrics, and phylogenetic comparative methods to reconstruct clade dynamics from the perspective of morphological evolution and disparification (Polly, 2004; Brusatte *et al.*, 2008; Drake & Klingenberg, 2010; Harmon *et al.*, 2010; Adams, Rohlf & Slice, 2013; Jones, Smaers & Goswami, 2015). Similar to Finarelli & Liow (2016), Polly *et al.* (2016) focus on the local processes that can have a dramatic effect on organismal evolution. Rather than taxonomic diversity, however, they examine morphological evolution, simulating the role of these smaller-scale processes in shaping clade dynamics through the lens of ecometric patterning, which is a means of describing and analyzing ways in which organisms track changing physical environments. Their analysis is performed at the community level, recording how species within a community track optimal environmental conditions, either by adapting through natural selection, diversifying through speciation or succumbing to extinction. The physical environment has a direct impact on species through factors such as ambient temperature, oxygen concentration, physical topography, predator abundance, and food quality. Species can respond to these varying drivers through their integument cover, gas exchange surfaces, locomotor morphology, and masticatory mechanics. Polly *et al.* (2016) explore the evolution of hypsodonty, increasing crown height of cheek teeth, in various plant-eating mammals through the Cenozoic, and test their data against numerous possible models. They find that phylogenetic structuring arose only when selection intensity, dispersal, and extirpation were all high. Ancestry and environmental geography produced historical effects on patterns of trait evolution and local diversity of species, although ecometric patterns appeared to be largely deterministic. Phylogenetic trait correlations and clade sorting appeared to arise more easily in changing environments than static ones. Microevolutionary parameters and historical factors both affected ecometric lag time and thus the balance between extinction, adaptation, and geographical reorganization as responses to climate change.

Simulations provide a powerful approach for reconstructing complex effects and generating hypotheses that can be tested with empirical data (Wagner, 2000; Polly, 2004; Hunt, 2012; Slater *et al.*, 2012; Goswami *et al.*, 2014). As the studies in this special issue demonstrate, the field of macroevolutionary research and the use of phylogenetic comparative methods have experienced vast growth in recent years. A large part of this increase may be attributed to the increasing availability of free software and code for running complex macroevolutionary

analyses, which has been (and should be) lauded. Indeed, many of the studies in this special issue describe new approaches, and provide the necessary code to run those methods, precisely to further expand the field of macroevolutionary analysis. However, with great analytical power comes great analytical responsibility, as Cooper *et al*. (2016) discuss in their contribution. Most methods for reconstructing trait evolution are based on Brownian motion models, which assume that trait variance is a function of time (e.g. branch length) and thus that similarity in form reflects closeness of relationship. Several expansions of this basic model have been developed over many years, including single and multiple Ornstein Uhlenbeck (OU) models and adaptive peak models, in which traits are drawn to certain optimal values rather than evolving randomly. Cooper *et al*. (2016) focus in particular on the use (and misuse) of OU models, simulating many common scenarios in which OU models are incorrectly preferred over simpler models. Of particular note is the sensitivity of this issue to measurement error and small tree size (and small is relative; they mean trees with fewer than 1000 tips). Because OU models have become a regular inclusion in macroevolutionary analyses, implemented in many common analytical packages, and because new multi-OU models will only exacerbate these issues by essentially splitting effective tree size with each additional peak, Cooper *et al*. (2016) make a strong argument for caution in the application of these methods without full consideration of their weaknesses, and they provide a useful list of recommendations to guard again misapplication and misinterpretation of OU models.

Smaers, Mongle & Kandler (2016) expand on our current toolkit for reconstructing trait evolution by describing a new adaptive-peak-based model for phylogenetic comparative analysis in which rates of evolution may vary on different branches. They note that most current formulations use the Brownian motion model as the null, in which the rate of evolution is stochastically constant across all branches, and that the average trait change is proportional to the square root of time. These assumptions, however, differ from the common view that different traits may evolve at different rates, and those rates may differ between subclades in a tree. In their new model, Smaers *et al*. (2016) allow evolutionary rates to differ along different branches of the phylogenetic tree, and they provide a multiple variance Brownian motion model as the null. In simulations, they show that their model can replicate results for a constant variance Brownian motion, and that, in cases where rates vary along different branches, their model outperforms the traditional model. In an empirical study of the evolution of the primate brain and body mass,

their model provides an improved statistical fit relative to other methods, and estimates of nodal values lie within the expected range based on the fossil record.

Baker *et al*. (2016) continue along this theme of variable rates in presenting a new approach for detecting exceptional shifts in the rate of phenotypic evolution, without the requirement of genetic data. Positive phenotypic selection is recognized where variation in the rate of morphological evolution is at least twice that of the background rate, and Baker *et al*. (2016) suggest that this is widespread and common in nature, demonstrating its presence in a wide range of organisms, including *Anolis* lizards, paravian (bird-line) dinosaurs, mammals (cetaceans and primates), and fleshy fruit angiosperms. Based on these findings obtained from a diverse sample of extant and extinct life, Baker *et al*. (2016) argue that episodic, rather than gradual, patterns in phenotypic macroevolution are the norm, dovetailing with the view from genetic studies, and indicating that analyses using simplistic evolutionary models based on homogeneous rates are likely to produce misleading results. Lastly, by enabling the recognition of rate heterogeneity without recourse to genetic data, the approach of Baker *et al*. (2016) allows the detection of deep time patterns of natural selection in taxa known only from fossils.

## MEASURING MORPHOLOGICAL DIVERSITY

Trait evolution is of course the precursor to the diversification of form, and studies of morphological diversity can provide a novel perspective with respect to both taxonomic diversity and evolutionary rates. Although all of these attributes may be aligned in certain scenarios, such as adaptive radiations, there are many cases in which evolutionary rates and disparity, or taxonomic diversity and disparity (Foote, 1993; Ruta *et al*., 2013), may be discordant. Measuring morphological disparity can take many forms, from univariate or multivariate continuous traits to discrete, or cladistics, traits. Each approach has its strengths and weaknesses, in terms of comparability, sensitivity to missing data (as is common with palaeontological datasets), and representation of organismal form, and all provide important information on how organisms diversify under different conditions (Foote, 1997). The next three papers approach the topic of morphological disparity with discrete character data, such as those commonly gathered for morphological phylogenetic analyses, providing an overview of measuring overall disparity, as well as an extension for examining trends in disparity, a detailed description and code for analyses of

morphological disparity, and a worked example focused on the archetypal adaptive radiation, the placental mammals after the end-Cretaceous mass extinction, 66 Mya.

As discussed in Hopkins (2016), there has been considerable work on morphological disparity using morphospaces to visualize changes in disparity through time, as well as quantifying these changes with metrics such as mean pairwise dissimilarity or overall morphospace occupation. However, she points out that directionality is frequently overlooked in studies of disparity, despite being the more emphasized aspect in studies of macroevolutionary trends. In this contribution, Hopkins (2016) analyses trends in morphological evolution in post-Palaeozoic echinoids and Cambrian pterocephaliid trilobites and demonstrates how observed trends within specific subclades can shape morphological disparity across clades. Long-term biases in both the direction of morphological evolution and the magnitude of change are observed to increase disparity through time in more inclusive clades, although not necessarily in the subclades exhibiting these trends. Increases in disparity in a large clade may also result from passive diffusion, or a combination of passive diffusion and active trends in only a small proportion of lineages or subclades. Thus, Hopkins (2016) demonstrates that understanding the mechanisms underlying morphological diversification benefits from an examination of directionality in morphological change, and not just its magnitude.

Lloyd (2016) continues on the topic of morphological disparity, as well as rate, as measured in a phylogenetic context using cladistic (i.e. discrete) character data. Cladistic data offer many advantages for large-scale analyses of morphological evolution because they are routinely gathered for phylogenetic analyses, usually attempt to maximize coverage of the organism's anatomy, and often are more comparable across very large clades than are morphometric data. They also benefit from having associated phylogenetic trees, which are important for many methods of macroevolutionary analysis. Lloyd (2016) provides a thoughtful, comprehensive, and practical guide for conducting analyses of disparity and evolutionary rate using cladistic data, and also introduces a new R package Claddis that can perform many of the described analyses. He conducts simulations to demonstrate which metrics are most accurate, and also develops a new, and potentially better, distance metric for analyses of cladistic data. As these fields grow, and discrete character datasets become increasingly available (as a result of the existing norm of publishing datasets for phylogenetic analyses), the useful discussion of issues such as time-scaling of trees, effects of missing data, and approaches to ordination is important for researchers new to this field, as well as for those who have been part of its development over the last few decades.

Finally, Halliday & Goswami (2016) return to the topic of adaptive radiations, and the significance of dramatic global events in shaping diversity. Employing the approaches discussed in Lloyd (2016), they assess phylogenetic measures of morphological disparity in Cretaceous–Paleocene eutherian mammals and provide support for a placental mammal adaptive radiation after the end-Cretaceous mass extinction (66 Mya). Utilizing an extensive phylogenetic data matrix of fossil eutherian taxa, including heavy sampling of Cretaceous and Palaeogene taxa, coupled with reconstructions of ancestral morphologies for all characters and nodes, Halliday & Goswami (2016) use the resultant distance matrix to calculate morphological range- and variance-based disparity. In the last two stratigraphic stages of the Cretaceous, Halliday & Goswami (2016) document an increase in total morphospace occupation from the Campanian to the Maastrichtian but a decrease in average dissimilarity among taxa. They interpret this as corresponding to a faunal turnover, where basal eutherians were replaced by taxa closer to the placental radiation. Morphospace range increases most strikingly immediately after the mass extinction, although mean dissimilarity lags behind, suggesting an adaptive radiation followed by later ecological specializations that resulted in increased dissimilarity through the early Palaeogene. Thus, although some changes in the eutherian fauna began in the Late Cretaceous, Halliday & Goswami (2016) provide substantial support for the Cretaceous/Palaeogene mass extinction having a dramatic effect on the evolution of eutherian mammals and leading to an adaptive radiation of placental mammals.

## CONCLUSIONS

The past few decades have represented a step-change in macroevolutionary research. New approaches and new sources of data in macroevolution and macroecology have enabled researchers to conduct robust quantitative tests of many long-standing debates in the evolution of biodiversity, and have also introduced new debates on methodological choices and important limitations of data and sampling. These massive changes in the study of clade dynamics through deep time are represented by the papers in this special issue, which explore speciation, trait evolution, and morphological diversity, comprising core components of any macroevolutionary study. They provide critical analyses of existing methods, descriptions and worked examples of new methods, and

novel applications of approaches borrowed from other fields of research. The result is a special issue that covers topics that are fundamental to macroevolutionary research and provides useful guides on analytical methods for new entrants to the field, as well as for seasoned veterans. We fully expect that this rapid progress in macroevolutionary research will persist well into the future, and we hope that this special issue will serve as a valuable resource for the next generation of macroevolutionary biologists as they continue to improve upon the work presented here.

## ACKNOWLEDGEMENTS

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