

Developmental push or environmental pull? The causes of macroevolutionary dynamics

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Abstract Have the large-scale evolutionary patterns illustrated by the fossil record been driven by fluctuations in environmental opportunity, by biotic factors, or by changes in the types of phenotypic variants available for evolutionary change? Since the Modern Synthesis most evolutionary biologists have maintained that microevolutionary processes carrying on over sufficient time will generate macroevolutionary patterns, with no need for other pattern-generating mechanisms such as punctuated equilibrium or species selection. This view was challenged by paleontologists in the 1970s with proposals that the differential sorting and selection of species and clades, and the effects of biotic crises such as mass extinctions, were important extensions to traditional evolutionary theory. More recently those interested in macroevolution have debated the relative importance of abiotic and biotic factors in driving macroevolutionary patterns and have introduced comparative phylogenetic methods to analyze the rates of change in taxonomic diversity. Applying Peter Godfrey-Smith's distinction between distributional explanations and explanations focusing on the origin of variation, most macroevolutionary studies have provided distributional explanations of macroevolutionary patterns. Comparative studies of developmental evolution, however, have implicated the origin of variants as a driving macroevolution force. In particular, the repatterning of gene regulatory networks provides new insights into the origins of developmental novelties. This raises the question of whether macroevolution has been pulled by the generation of environmental opportunity, or pushed by the introduction of new morphologies. The contrast between distributional and origination scenarios has implications for understanding evolutionary novelty and innovation and how macroevolutionary process may have evolved over time.

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1 Introduction

The factors generating large-scale evolutionary patterns as documented in the fossil record have long been a concern to biologists and have generated a wide range of views on the relative importance of driving factors such as natural selection, climate change or extinction. Long before, naturalists like Darwin, Cuvier, Buffon and others had already clashed over whether biotic extinction had actually occurred (Rudwick 2008). Chapter 9 of *The Origin of Species* was titled: “On the Imperfections of the Fossil Record”, in which Darwin argued that the absence of expected intermediate forms, episodic sedimentation and the sudden appearance of animal fossils (now recognized as the Ediacaran–Cambrian radiation) each reflected the inadequacies of the fossil record rather than a real signal of evolutionary pattern (Darwin 1859). Through the later nineteenth century and early twentieth century some paleontologists argued that apparent evolutionary trends were evidence for an alternative evolutionary theory with internal drive (known as orthogenesis; see Osborne 1922; Bowler 1992). Such non-Darwinian arguments diminished with the advent of the neo-Darwinian synthesis in the early 1940s. Discussions over the origin of higher taxa became a proxy for broader issues about the relationship between macroevolution and microevolution (Huxley 1958; Simpson 1959; Mayr 1960; Schaeffer and Hecht 1965; Bock 1979).

Darwin’s argument about the inadequacies of the fossil record was largely accepted by paleontologists and evolutionary biologists into the 1970s, when Gould and Eldredge argued that the episodic pattern of speciation in Devonian trilobites and Bermudan land snails might be real (Eldredge and Gould 1972). In contrast to Simpson’s support of the Modern Synthesis as a sufficient explanation of large-scale evolutionary patterns, later paleontologists argued that macroevolution required a distinctive suite of mechanistic explanations (Eldredge 1979, 1985; Stanley 1975, 1979; Gould 1980b; Valentine 1980; Sepkoski 2012).

Two different classes of evolutionary explanation have been distinguished: those that focus on origin of evolutionary variation, and a second class that assumes the existence of variants but assigns the driving force to their differential distribution or success (Godfrey-Smith 2014). While the role of selection in the differential reproductive success of individuals within populations has been generally accepted, Godfrey-Smith notes that since the late nineteenth century there has been controversy over the importance of selection in origins explanations (Bowler 1992). He then goes on to mount a spirited (although I think not all together convincing) defense of the relevance of selection to origins explanations. Macroevolutionary approaches have been similarly divided between origins and distributional explanations. When Filipchenko introduced the term macroevolution he was focused on mechanisms that generated large-scale morphologic changes: an origins explanation (Filipchenko 1927). Goldschmidt shared this interest

(Goldschmidt 1940), as did Gould when he was focused on the role of development (Gould 1977, 1982). However, ever since Dobzhansky (a student of Filipchenko's in Russia) introduced the term macroevolution to western evolutionary biologists (Dobzhansky 1937) and since its popularization by Simpson (Simpson 1944) it has primarily been applied to distributional explanations of evolutionary patterns. This emphasis on distributional explanations has continued through the past several decades.

This distinction between origins and distributional explanations for macroevolutionary patterns is reflected in another difference in evolutionary perspective: a focus on ecological opportunity is central to the views of Simpson, Mayr, many of those who work on adaptive radiations (e.g. Losos 2010; Stroud and Losos 2016) and much contemporary macroevolution research. The alternative proposed by advocates of comparative studies of the evolution of development (“evo-devo”) is that the generation of new morphological variants through repatterning of developmental regulatory processes generates new morphologies (Carroll 2008; Brakefield 2011; Lowe et al. 2011). Developmental biologists are often not so much opposed to a role for ecology as they simply ignore it.

The term macroevolution is thus used in two different senses: as a description of large-scale patterns and as an argument for processes associated with origin and distributional sorting of taxa distinct from microevolutionary processes. This contribution begins with a review of the scope of macroevolutionary problems. Next I survey arguments that macroevolutionary patterns can be subsumed without remainder in microevolutionary processes, and then contrast macroevolutionary explanations that address distributional processes with those that focus on origins. This leads to a discussion of evolutionary novelty and innovation, two of the key aspects of macroevolutionary patterns. Another way of viewing the differences between distributional and origins explanations is that the former emphasize the importance of ecological opportunity (“ecological pull”) while the latter focuses attention on the generation of novel phenotypes (“developmental push”).

2 The scope of macroevolutionary patterns

One perspective on the place of macroevolution within evolutionary biology is available through examining large compendia. Pagel's two-volume *Encyclopedia of Evolution* (Pagel 2002) includes an essay on macroevolution by Gould that examines distinctive macroevolutionary phenomena, including historical contingency, evolutionary trends and the significance of mass extinctions (Gould 2002a). One might have expected that a volume grandly titled *Evolution: The First Four Billion Years* and published to coincide with the bicentennial of Darwin's birth and the sesquicentennial of the publication of *The Origin* (Ruse and Travis 2009) might include paleontology. Although the book does include an essay on the history of life, macroevolution only appears in a few topical entries on adaptation, evolution and development, and biographical entries on Steve Stanley and on Gould. In contrast, Losos's *Princeton Guide to Evolution* contains over 100 pages largely

focusing on speciation, but including essays on adaptive radiations, macroevolutionary rates and trends, extinction, species selection and innovation (Losos 2014).

Since the advent of the Modern Synthesis in the 1940s speciation has formed a hinge point between micro- and macroevolution with some authors including it in microevolution, others in macroevolution. Here I will follow most paleontologists and restrict macroevolution to evolutionary patterns from the species level and above (Eldredge and Cracraft 1980; Gould 2002b; Myers and Saupe 2013; Futuyma 2015). Thus macroevolutionary patterns include speciation, evolutionary trends, adaptive radiations and other evolutionary diversifications. Simpson argued that the entire history of life involved adaptive radiations and evolutionary trends (Simpson 1960), encompassing events as disparate as the Cambrian radiation of animals and diversifications of restricted clades, whether angiosperms, placental mammals or silverswords on the Hawaiian Islands. I have recently argued that evolutionary diversifications involve much greater variety of pattern and process than suggested by Simpson (Erwin 2015). The expanded interest in mass extinctions following the proposal of an extraterrestrial impact associated with the Cretaceous-Paleogene event (Alvarez et al. 1980) led to studies of whether such biotic crises selectively filter the biota via different rules than prevail during the background intervals between extinctions (Gould 1985; Jablonski 1986, 2005).

The question of whether there are distinctive macroevolutionary processes that differ from those responsible for microevolution has long generated controversy. Simpson's work emphasized the continuity between macroevolutionary patterns and microevolutionary process. Beginning with the proposal of punctuated equilibrium in the 1970s a number of paleontologists invoked the possibility of a decoupling between intra- and supra-specific processes (Eldredge and Gould 1972; Stanley 1975, 1979; Eldredge 1979; Valentine 1980; Valentine and Erwin 1983). In one of the most influential articulations of distributional decoupling Gould distinguished three evolutionary tiers: ecological processes of the first tier, or what he termed "the struggle among organisms at ecological moments"; the origin of species and the formation of evolutionary trends at the second tier, including his model of speciation via punctuated equilibria; and episodes of mass extinction for the third tier (Gould 1985, p. 2). Gould argued that the processes within each tier are essentially independent of those in the other tiers. (A fourth tier was later proposed by the insertion of inter-population dynamics associated with glacial-interglacial cyclicity; see Bennett 1990). Later work emphasized the hierarchical structuring of evolution (Vrba and Eldredge 1984; Cracraft 1985; Valentine and May 1996; Jablonski 2007) with species as distinct evolutionary individuals and thus necessarily decoupled from intra-specific change (Hull 1980), distinctive survival patterns of genera during mass extinctions relative to background intervals (Jablonski 1986, 1989, 2010), and selection operating at the level of species (Stanley 1975; Cracraft 1985; Vrba 1989; Gould 2002b; Jablonski 2008).

Historically, macroevolutionary origins explanations have been associated with the saltational views of Goldschmidt (1940), and the derision heaped upon him by generations of microevolutionists was long sufficient to dissuade others from invoking similar scenarios (although there have been periodic forays into macroevolution; see e.g. Bateman and DiMichele 1994; Theissen 2006; see

discussion in Futuyma 2015). But the neglect of developmental biology during the modern synthesis, and growing evidence for the importance of developmental repatterning in evolution (Britten and Davidson 1971; Gould 1977; Bonner 1982), increased interest in describing morphological changes reflecting developmental evolution (heterochrony). In addition, the discovery of the extent of deeply conserved genes across animals (and later across plants and various higher eukaryotes) has generated renewed interest in the genetic and developmental sources of phenotypic variation, distinct from mutation. Developmental or internal constraints on evolutionary trajectories provide a third avenue of explanation (Maynard Smith et al. 1985; Reif et al. 1985; Losos 2011).

Origins explanations could provide another source of uncoupling between microevolution and macroevolution if there are different sources of variation for macroevolutionary changes in morphology, such as the novelties associated with the establishment of major clades (Moczek 2008; Peterson and Müller 2013). For example, polyploidy and some types of repatterning of developmental gene regulatory networks (GRNs) have been proposed as drivers of macroevolutionary change. One of the challenges for any macroevolutionary origins explanation is that many microevolutionists view *any* mechanism associated with the generation of variation as *de facto* microevolutionary. The flexible boundaries of microevolution create challenges for distinguishing macro- and microevolutionary processes, a difficulty also faced by those who distinguish evolutionary novelty from adaptation (Wagner 2014).

3 Explanations from microevolutionary processes

At least since the Modern Synthesis, most evolutionary biologists have assumed, often implicitly, that macroevolutionary patterns were generated by microevolutionary processes. Historically, this argument makes considerable sense. The late nineteenth century and the first decades of the twentieth century saw the propagation of an array of theories that rejected natural selection, including orthogenesis and various macromutationist views. One could argue that extrapolating macroevolutionary pattern from microevolutionary processes may have been important to the success of the neo-Darwinian synthesis beginning in the 1930s. Futuyma (2015) makes the fair point that critics of the ‘hardening’ of the modern synthesis sometimes neglect the widespread rejection of natural selection and adaptation into the 1930s and the challenges faced in developing a scientifically rigorous field of evolutionary biology.

Nonetheless, the argument that one could extrapolate from microevolutionary processes to explain macroevolutionary patterns was a core claim of the Modern Synthesis, although the perspectives of some of the major contributors to the synthesis differed considerably. In the final chapter of Mayr’s (1942) contribution he argued that “all the processes and phenomena of macroevolution and the origin of the higher [Linnaean] categories can be traced back to intraspecific variation” (Mayr 1942, p. 298). Dobzhansky was more agnostic, writing in a well-known comment that “there is no way toward an understanding of the mechanisms of

macroevolution, which require time on a geological scale, other than through a full comprehension of the microevolutionary processes... For this reason, we are compelled at the present level of knowledge reluctantly to put a sign of equality between the mechanisms of macro- and micro-evolution” (Dobzhansky 1937, p. 37) Similarly, although Simpson distinguished macroevolutionary and megaevolutionary patterns from microevolutionary patterns, he also asserted that in the absence of further evidence one should assume that all these patterns were generated by microevolutionary mechanisms: “Macro-evolution involves the rise and fall of discontinuous groups, and it is still debatable whether it differs in kind or only in degree from micro-evolution. If the two proved to be basically different, the innumerable studies of micro-evolution would become relatively unimportant and would have minor value in the study of evolution as a whole” (Simpson 1944, p. 97). Indeed, it is just such claims of discontinuity which have fueled the rise of macroevolutionary approaches since the 1980s (as discussed in the next section). Perhaps the most nuanced view of macroevolution from a contributor to the Modern Synthesis was Bernhard Rensch’s *Evolution above the Species Level* (Rensch 1959 [1954]). Futuyma describes Rensch as “the great unsung hero of the evolutionary synthesis” (Futuyma 2015, p. 35). Rensch provides a remarkably modern overview of macroevolutionary issues, from diversification into new habitats and evidence from the fossil record to discussions of development and the role of inadequate fossil preservation in generating apparent sudden changes in morphology. Ultimately however, Rensch, like all of his Modern Synthesis colleagues, focuses on the issue of macromutation as the critical question in macroevolution, concluding that microevolutionary processes appear sufficient to explain macroevolutionary patterns. The possibility of distributional macroevolutionary processes, from punctuated equilibrium to species selection and the effects of biotic crises, was not evaluated by Mayr, Dobzhansky, Simpson or Rensch. Decades of subsequent microevolutionary studies have demonstrated the power of natural selection, the importance of drift at small population sizes, and the complexities of speciation processes.

Thus, there are three issues where macroevolution could challenge the explanatory primacy of microevolution: First, the issue of discontinuities, whether via speciation, species and clade selection or biotic crises. Second, standard evolution largely lacked a theory for the origins of variation because it focused on the vertical transmission of information between generations by changing allele frequencies (Amundson 2005). Mechanistic developmental biology provided a robust characterization of how genomic information was translated, through development, and particularly through gene regulatory networks (GRNs), into the phenotype (Carroll 2005, 2008; Davidson 2006). This suggests that there may be differences in the types of variation that underpin adaptive evolutionary change from some types of abrupt phenotypic change. This need not involve ‘macromutations’ as described by early Mendelians or Goldschmidt, but is rather a recognition that developmental biology has documented greater complexities in the developmental production of the phenotype than suggested by early models of genotype to phenotype mapping. Finally, although both Simpson (1959) and Mayr (1960) addressed the issue of evolutionary novelty, this topic has been greatly neglected

from the synthesis into the 1990s. The remainder of this paper focuses on these three issues within the framework of distributional and origins-based explanations.

4 Explanations based on distributional processes

The resurgence of macroevolutionary approaches to the fossil record from the 1970s largely focused on distributional questions, particularly potential discontinuities between intra-specific adaptation and the generation of species or trends within a clade of species. Gould and Eldredge's punctuated equilibria model of speciation posited that speciation involved only a brief part of the history of a species, and began as an application to the fossil record of Mayr's peripatric model of speciation (Eldredge and Gould 1972; Gould and Eldredge 1993). The broader implications of the punctuated equilibria theory were first discussed by Stanley, who described species selection as analogous to natural selection, but operating on the "largely random process of speciation" (Stanley 1975, p. 646). Studies of macroevolution exploded during the 1970s and 1980s, but proved highly controversial among other evolutionary biologists, with many rejecting claims for distinct processes acting at the level of speciation or above.

This is not the place for a detailed history of macroevolutionary studies (but see Gould 2002b; Jablonski 2005, 2007; Sepkoski 2012; Myers and Saupe 2013). Rather, I want to briefly identify four major research themes which have informed studies in distributional macroevolution. The first of these themes grew out of the work of Gould, Eldredge and Stanley, focusing on issues of differential sorting and selection of species as a form of discontinuity between micro- and macroevolution (Vrba 1984; Jablonski 2008). A recent meta-analysis of species-level patterns of trait evolution compared the fit of models of directional change, stasis and a random walk, showing that few studies exhibited directional evolution with the majority evenly split between random walks and stasis (Hunt 2007). A subsequent, enlarged analysis reached the same conclusion (Hopkins and Lidgard 2012). A variety of mechanisms have been proposed to account for the dominance of stasis and random walks, but a consensus has not been achieved (Hunt and Rabosky 2014). These results also have implications for understanding the mechanisms underlying macroevolutionary trends: if directional trends are rare at the species level, then driven macroevolutionary trends (*sensu* Wagner 1996; McShea 1998) should also be rare.

The recognition that mass extinction events and smaller biotic crises could derail evolutionary patterns during 'background' intervals between such events added a further disconnect between micro- and macroevolutionary processes (Gould 1985; Jablonski 1986). There have been only five or six major mass extinctions over the past 500 million years (Sepkoski Jr. 1986), but there have been many more biotic crises (Bambach 2006). Mass extinctions may filter species and clades based on criteria other than those operating during background times, and thus may reset the assemblage of clades, ecological and functional interactions, and other attributes (Wagner et al. 2006; Erwin 2008a).

A third major research theme in distributional macroevolution has addressed global biodiversity trends through the Phanerozoic, particularly among marine animals (Sepkoski Jr. 1981, 1984, 1988, 1993, 1997; Alroy et al. 2001, 2008; Alroy 2010; Sepkoski 2012, 2013), but also among terrestrial vertebrates (e.g. Friedman and Sallan 2012; Brusatte et al. 2010), plants (Niklas et al. 1985; Magallon and Castillo 2009), and insects (Labandeira and Sepkoski 1993). Recognition that these global patterns are subject to a variety of potential biases, including variation in the amount of fossiliferous rock and sampling effort, has led to a number of attempts to adjust for such biases (Alroy et al. 2001; Peters and Foote 2001; Smith et al. 2012).

These three major research themes, of species-level processes, mass extinctions and global diversity patterns, have fueled a rich exploration of macroevolutionary pattern and processes since the 1970s. More recently a fourth theme has emerged from the analysis of data preserved in the topology of phylogenetic trees. As such trees have become more reliable, and have encompassed larger clades, they have enabled the analysis of changing pattern of diversity within a phylogenetic rather than purely taxonomic framework (Nee and May 1997; Ricklefs 2004; Harmon et al. 2010; Rabosky 2013; Slater 2015). In particular, these methods have improved models of character trait evolution. Phylogenetic comparative methods have also been combined with morphologic and molecular data to analyze patterns of diversification. For example, teleost fish are highly diverse (~ 29,000 living species) compared to the holosteians, the sister clade to the teleosts, comprising eight living species of gars and bowfins only. Yet despite claims for greater phenotypic evolution among teleosts, analysis of fossil and recent data, has revealed that holosteian phenotypic evolution was just as rapid as teleosts during the first 160 million years (Clarke et al. 2016).

Among the most trenchant questions raised by these approaches to distributional macroevolution is the relative importance of biotic and abiotic factors: First raised as Van Valen's 'Red Queen' hypothesis (Van Valen 1973), in which biotic interactions are a primary driver of evolutionary dynamics, others have suggested that abiotic forces, including climate and other environmental factors, may be the most important drivers (Benton 2009; Moen and Morlon 2014; Myers and Saupe 2013; Voje et al. 2015). There may be no general resolution to this controversy, with the relative importance of biotic and abiotic factors varying depending on the setting, the taxa involved, and the question under investigation. What is often not sufficiently appreciated is the difference in scale between biotic and abiotic forcing factors: many abiotic factors reflect global or near-global influences while biotic factors operate on local to regional scales. Thus during intervals in which abiotic factors are highly influential analyses of global diversity may be meaningful. In contrast, during intervals in which biotic factors dominate global diversity is simply a summation of local and regional processes and thus may not be particularly informative.

5 Explanations based on the origin of macroevolutionary variation distinct from microevolutionary variation

The role of origins explanations in macroevolutionary processes dates at least to the late nineteenth century in the form of macromutationist and orthogenic views, which continued with the saltationist views of geneticist Goldschmidt (1940), and the mutation-driven evolution of German paleontologist Otto Schindewolf (1994 [1950]). Despite Gould's efforts to rehabilitate Goldschmidt (Gould 1980a) the view that major evolutionary events were driven by mutations generating 'discontinuous' transitions in morphology was largely ignored during the Synthesis (see discussion by Futuyma 2015). The resurgence of interest in the role of development in evolution was due, at least in part, to publication of Gould's *Ontogeny and Phylogeny* (Gould 1977) and the associated interest in the role of heterochrony in macroevolution (Gould 1982; Alberch 1982; Bonner 1982; Love 2003). Futuyma (2015) provides a succinct history of the engagement of developmental biologists with the synthesis.

While the study of comparative embryology began in the 1800s, a coherent theory of the origins of evolutionary variation only began with the discovery of the information-carrying role of DNA in the 1950s, with early models of gene regulation (Jacob and Monod 1961; Britten and Davidson 1971), and increased significantly with the origins of comparative developmental biology (evo-devo) (Carroll et al. 2001; Wilkins 2002; Love 2003; Laubichler and Maienschein 2009). Early evo-devo studies identified highly conserved genes across Bilateria (and later across Metazoa) and expanded into analyzing patterns of gene expression. The elucidation of regulatory pathways (sometimes termed 'devo-evo' to contrast it with expression studies) has provided an increasingly mechanistic understanding of such changes (Davidson 2006; Carroll 2005, 2008; Peter and Davidson 2015). There is continuing controversy, however, over the extent to which our greatly expanded understanding of developmental biology has challenged approaches to macroevolution. As many authors have recognized, much of the early excitement about evo-devo stemmed from the insights provided into the origins of macroevolutionary patterns: the origin of animals, the origin of vertebrate limbs, and related questions. It was less clear, however, that these discoveries required a re-examination of macroevolutionary approaches to the origins of variation. Some evolutionary biologists have argued that the insights from comparative developmental studies are entirely consistent with microevolutionary approaches (Hoekstra and Coyne 2007; Futuyma 2015), while others, both developmental biologists (Carroll 2005, 2008; Davidson 2006) and paleobiologists (Shubin et al. 2009) have emphasized the distinct nature of regulatory repatterning as a source of evolutionary variation. (Regrettably, this issue has become conflated with discussions over the adequacy, or not, of the Modern Synthesis, an issue which I do not address here).

A major source of paleontological support for origins explanations comes from quantitative studies of morphologic diversity (also known as disparity), instigated by Gould's book on the Cambrian Burgess Shale fossils, *Wonderful Life* (Gould 1989). Such studies have generally confirmed earlier intuitions that major increase

in within-clade disparity occur early in clade history (the ‘early-burst’ model) and are decoupled from increased taxonomic diversity (Foote 1997; Erwin 2007; Hughes et al. 2013; Ruta et al. 2013). When disparity increases more rapidly than taxonomic diversity the extent of morphologic changes between ancestor and descendent would appear to have been greater than later in lineage history. This at least suggests a biased pattern of the success of major morphological changes. Whether this is actually a difference in the relative success of these phenotypic changes rather than their generation, however, awaits more rigorous study.

Many results from evo-devo studies are entirely consistent with microevolutionary approaches to evolution. But there remains an unresolved issue of whether the sources of genomic and developmental changes which generate some types of phenotypic variation, such as the novelties associated with the origins of major clades, differ from those that underpin traditional microevolution?

6 Novelty and innovation

Nothing in evolutionary biology better illustrates the conflation of distributional and variational processes, and the continuing tension over the appropriate nature of evolutionary explanation, than debates over the origins of phenotypic novelties and innovations (Moczek 2008; Brigandt and Love 2012). These terms are often used interchangeably, but evidence that long lags may be found between the origin of a novelty and its ecological and evolutionary success demonstrates that these are two distinct phenomena (Erwin and Valentine 2013; Erwin 2015). Novelty refers to the origin of new, individuated and quasi-independent phenotypic characters, rather than variations upon preexisting characters (Wagner 2014). Wagner tied novel characters to distinctive gene regulatory patterns [which he called character homology identity networks (ChINs) and which are identical to the structures that Davidson and I termed kernels; see Davidson and Erwin (2006)]. I prefer to leave the nature of the underlying structure of gene networks as a hypothesis rather than as part of the definition of novelty. In addition, defining novelties as individuated characters allows the term to be applied to a wide range of settings, from microbes to new mechanisms of genetic control, such as the origin of distal enhancers (Sebe-Pedros et al. 2016), to aspects of cultural evolution. Thus novelties are associated with the generation of new phenotypic variants, but variants that represent individuated characters rather than character states; for example, the origin of feathers but not the huge variety of feathers that evolved subsequently. Similar examples of novelties include the vertebrate limb, the bat wing, or the compound eye of arthropods (Strausfeld et al. 2016).

In contrast, innovation reflects the ecological and evolutionary success of a phenotypic novelty. Distinguishing between novelty and innovation is critical because the two are not necessarily linked. Long, macroevolutionary lags between the generation of novel phenotypes and their evolutionary success are not uncommon, and have been identified in a number of clades (Erwin 2015). Most participants in the modern synthesis tied the appearance of morphological novelties to ecological opportunities, while recognizing the complexities of the process (Mayr

1942, 1960; Simpson 1944; Miller 1949). But if the success of a clade is decoupled from the origin of the novelty, then ecological opportunity may be of little import.

Although phenotypic novelty and innovation encompasses only a small portion of evolutionary events, and even a fairly small portion of macroevolutionary events, they have had a disproportionate impact by establishing the major themes in the history of life.

7 Discussion

Distributional macroevolutionary mechanisms reflect the response of organisms and clades to environmental opportunities and pressures. Until recently organisms were often viewed as passively responding to these opportunities and pressures (a view that extended from Simpson to Gould). The recognition that organisms often actively modify their environment to produce fitness effects (niche construction; see Post and Palkovacs 2009; Matthews et al. 2014) and that this may have macroevolutionary effects (Erwin 2008b) adds another level of dynamism to macroevolutionary processes. Nonetheless, distributional macroevolution has focused almost exclusively on the differential sorting of species and clades once they have arisen. Insights from evo-devo demonstrate that the range of variation feeding into macroevolutionary dynamics may be broader than previously recognized. Macroevolutionary lags illustrate the disjunction between the supply of morphological novelties and their subsequent ecological and evolutionary success as evolutionary innovations. But macroevolution covers a much broader array of patterns than novelty and innovation, and many cases of high early disparity in a clade, even if these do not involve morphologic novelties, may still represent the biased origination of phenotypic variation.

The evolutionary process has itself evolved over time through the introduction of new regulatory mechanisms that generate new phenotypic opportunities, and via intrinsic and extrinsic constraints, although this was not recognized either by advocates of the Modern Synthesis, nor by paleontological discussants of macroevolution from the 1970s onward. The population genetic foundations of the modern synthesis are ahistorical and there is no obvious reason why the components of distributional macroevolution (punctuated patterns of speciation, species selection, evolutionary trends and mass extinctions) should change over time. In contrast, however, a number of conceptual developments since the 1990s have challenged the widespread, often implicit assumption of evolutionary uniformitarianism (Erwin 2011) and suggest evolutionary changes to the origins of variation that may have had far-reaching evolutionary effects. When Maynard Smith and Szathmary proposed the concept of major evolutionary transitions they recognized that the origin of new evolutionary individuals during these transitions were evolutionary discontinuities (Maynard Smith and Szathmary 1995; see also Calcott and Sterelny 2011; Szathmary 2015). Patterns of variability of characters (evolvability) and modularity (Wagner and Altenberg 1996; Kirschner and Gerhart 1998; Wagner et al. 2007) need not necessarily vary systematically over time, but if they do systematic biases could result. Finally, evolution in the structure of GRNs

may change the types of accessible variation over time, reflecting systematic changes in the evolutionary lability of different components of the network (Davidson and Erwin 2006; Erwin and Davidson 2009).

Whether evolutionary theory needs to be reformulated and extended has provoked considerable controversy (Hoekstra and Coyne 2007; Pigliucci 2009; Laland et al. 2015; Futuyma 2015) but may be largely beside the point. Our understanding of evolution has become incomparably richer over the past few decades as the intellectual hegemony of population genetics has faded. This is particularly true when considering macroevolutionary patterns. Macroevo­lutionary dynamics are both pushed by the origin of new phenotypes via developmental processes, as well as pulled by changes in climate and other aspects of the physical environment and biotic factors such as adaptive divergence and niche construction. The challenge moving forward will be to establish the relative importance of developmental push and environmental pull, the specific conditions under which each plays a significant role, and whether the relative contributions of development and environment have changed over time.

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