Novelties That Change Carrying Capacity

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ABSTRACT
Comparative developmental studies have revealed a rich array of details about the patterns and processes of morphological change in animals and increasingly in plants. But, applying these insights to the study of major episodes of evolutionary innovation requires understanding how these novel morphologies become established and sufficiently abundant (either as individuals within a species or as a clade of species) to be preserved in the fossil record, and, in many cases, to influence ecological processes. Evolutionary novelties may: (1) disappear without changing the species; (2) be associated with the generation (through selection or drift) of a new species; and if the latter (3) may or may not become ecologically significant. Only the latter are commonly preserved in the fossil record. These alternatives mirror the distinction among historians of technology between innovation and invention. Here, I argue that specific sorts of evolutionary inventions drive ecological transformation, essentially constructing an environment for themselves and ancillary organisms through ecological spillover effects, increasing the "carrying capacity" of an ecosystem. *J. Exp. Zool. (Mol. Dev. Evol.) 314B, 2011.* © 2011 Wiley-Liss, Inc.

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Historians of technology have traditionally made a distinction between invention and innovation, a distinction that could profitably be adopted by biologists. Invention, in this sense, is the creation of something new: a new object, product, process, or item that could be patented or was otherwise not previously known. Many inventions are of course just slight variations of existing objects, rather than fundamentally new creations. Others are new combinations of pre-existing components, perhaps modified for a different purpose (Arthur, 2009). In contrast, innovations are successful inventions: successful in the sense that they are actually put into production and become economically useful. (Useful here in the sense of making money rather than necessarily providing value.) Patent databases reflect only a fraction of actual inventions, but most patents never become successful innovations.

The distinction between invention and innovation mirrors the situation in evolution. The origin of novelties is an important topic for evo-devo (Muller and Wagner, '91; Love, 2003; Saenko et al., 2008) and is the topic of other contributions here [Hall and Kerney (this issue) and Hallgrimsson et al. (this issue)]. Indeed, one of the primary contributions of work in comparative evolutionary developmental biology has been to focus on the generation of variation, particularly through modifications of

developmental processes, in contrast to the almost exclusive focus of population geneticists and most of the Modern Synthesis on the differential sorting of variation by drift and selection (Amundson, 2005). The intriguing question for comparative evolutionary developmental biologists is whether the nature of variation revealed by evo-devo studies differs substantially from that envisioned by models of population genetics. To the extent that it does, evo-devo may represent an important challenge to evolutionary theory. Many recent discussions of an emerging new evolutionary synthesis hinge upon just this issue (Muller, 2007; Pigliucci, 2007, 2009; Carroll, 2008), although it has often been framed as a discussion about the importance of cis regulatory changes vs. the evolution of structural genes.

But, the generation of novelty no more guarantees that the new variant will become successful than does acquisition of a patent presage economic success. The missing piece in our discussions is how these developmental novelties (inventions) become ecologically and evolutionarily successful innovations. If we are primarily interested in evolutionary novelties that become established, successful species, and particularly those that become sufficiently abundant, widespread, and long lasting to be found in the fossil record, then we must also address the ecological and evolutionary processes between the generation of evolutionary novelties and the success as species, and even as the foundation of new clades. Such issues have been addressed within the context of phenotypic plasticity. The temptation is to consider developmental evolutionary innovations as simply another form of variation, with the subsequent steps in the chain no different than any in other speciation event.

Here, I challenge this assumption. In contrast to the predominant emphasis on the generation of variation, I address the factors that contribute to the ecological, and thus evolutionary, success or failure of novel morphologies. In particular, as a paleontologist, I am largely concerned with the macroevolutionary aspects of this question, rather than the generation of new population-level variation. I begin by addressing in turn the processes of fixation of evolutionary novelties within a population, speciation, and the establishment and diversification of a new clade. One question in which I am interested is whether evolutionary innovations generated by changes in development gene regulatory networks (GRNs) (Davidson and Erwin, 2006, 2010; Erwin and Davidson, 2009) may be particularly responsible for the Ediacaran–Cambrian diversification of early animals (580–510 Ma [million years ago]), but the issues raised here also apply to other major evolutionary innovations, such as the early diversification of land plants in the Devonian–Carboniferous (416–299 Ma), the explosive diversification of vertebrates following the end-Permian mass extinction (252 Ma) and placental mammals following the Cretaceous–Tertiary mass extinction (66.5 Ma). Thus, the later portion of this article will address both the developmental and ecological involvement of evolutionary novelties that may modify the "carrying capacity" of an ecosystem. The critical issue is whether developmental innovations can drive ecological changes that enhance the probability of success of the innovations, or, with apologies to G. Evelyn Hutchinson, can development help construct the ecological theater for the evolutionary play?

PERSISTENCE OF EVOLUTIONARY INNOVATIONS

Many discussions of the role of development in evolutionary innovations focus on the generation of variation, implicitly assuming that the success of such innovations will be driven by selection or drift; but many of these discussions do not address the processes of population dynamics that necessarily influence the termination or persistence of such innovations. Such myopia may have influenced the debates between the evo-devo community and population geneticists as much as disagreements over the relative evolutionary importance of regulatory and protein-coding genes (e.g. Carroll, 2005; Hoekstra and Coyne, 2007). One area that has received considerable attention, however, is the role of pleiotropy in the differential success of different types of changes; for example, changes in coding sequences vs. cis regulatory changes and whether the probability of fixation of adaptive changes decreases with increasing organismal complexity (Orr, 2000). However, recent studies reveal that genetic interactions are highly modular, and thus that pleiotropy is less of a restriction to adaptive evolution than had been proposed (Wagner et al., 2008; Streisfeld and Rausher, 2010; Wang et al., 2010; Wagner and Zhang, 2011). These studies have examined a particular component of GRNs—those at the proximal end. More importantly, perhaps, it seems to me critical to address whether particular types of developmental changes may play out differently over evolutionary time because of the nature of the change. For example, Davidson and I proposed that a specific class of cis regulatory changes were haplosufficient and could readily spread within a population, providing populations with high fecundity (such as spawning marine invertebrates) with a means of "experimenting" with developmental changes at a high rate, but at relatively low cost (Davidson and Erwin, 2010).

In principle, evolutionary novelties may: (1) occur within a population, but disappear without becoming fixed in either the population or the species; (2) become fixed within a population or species and be associated with the generation (through selection or drift) of a new species. Because of the negative relationship between effective population size and drift, it is important to recognize that the appearance of novel morphologies, particularly during evolutionary radiations, cannot simply be assumed to reflect greater fitness. In addition, some taxa may differ considerably in morphology but be functionally identical (Wainwright, 2009). Some, perhaps even many, evolutionary novelties are associated with new species or clades and are of interest because they are morphologically distinctive. Many of the oddities of the early and middle Cambrian Chengjiang and Burgess Shale Faunas have attracted so much attention simply because they are so weird looking; and finally, (3) even if morphologic novelties are associated with new species, the new species may or may not become ecologically significant. Because the fossil record is largely composed of taxa that are readily preserved, abundant and geographically widespread (factors that increase the likelihood of both preservation and subsequent recovery) ecologically significant taxa are more likely to be commonly preserved in the fossil record, if durably skeletonized. (There are many ecologically significant taxa with little or no fossil record because they have poor preservation potential.)

IMPLICATIONS FOR SPECIATION

Spread and fixation of novelties within a population or species is generally a prerequisite for evolutionary significance. Although

this is not a central focus of this article, it is worth noting the lack of attention whether developmental innovations are subject to distinct population processes from the mutations in structural genes. Selection certainly plays a significant role in the fixation and persistence of evolutionary novelties, yet recent articles have suggested that the roles of mutation pressure (Nei, 2007) and drift may have been downplayed. In particular, Lynch has emphasized the critical role of effective population size in evolutionary events, noting that at small N_e ($<$10,000) drift may swamp the effects of selection (Lynch and Conery, 2003; Lynch, 2007). Because population size is generally negatively correlated with body size, it is particularly likely that the origin of clades with larger body size may have been heavily influenced by drift rather than selection. Population size may also be small, even for small organisms, early in the history of a clade. Although it can be difficult, if not impossible, to understand the population dynamics of species in the distant past, the role of population size must nonetheless be considered in evaluating the processes responsible for the persistence of evolutionary novelties.

In addition, the success of modern studies of transcription factors provides at least one suggestion that there may be important differences in the processes involved in evolutionary changes in development. Many gene co-options of transcription factors are gain-of-function mutations (indeed, if this were not true, many developmental studies would be impossible) (Ruvkun et al., '91; Davidson, 2009). Consider then a marine organism producing abundant planktotrophic larvae: gain-of-function mutations could have a high rate of production, much like variant antibodies. This has the potential to generate rapid and extensive evolutionary change, but via a different route than the traditional concern with fixation of mutants within a population. Indeed, given the potential for rapid evolutionary change by gain-of-function gene co-option, the difficulty may be more with limiting the rate of change than anything else (Davidson and Erwin, 2009).

ECOLOGICAL OPPORTUNITY IN EVOLUTIONARY RADIATION

Much of our view of diversification is based upon classic views of adaptive radiation: the diversification of species within a single clade, as exemplified by Darwin's finches in the Galapagos, and similar events (Simpson, '53; Schluter, 2000). Following Simpson, discussions of adaptive radiations have focused on the importance of ecological opportunity in facilitating the diversification. Both biologists and paleontologists have taken this as a model for other diversification events, from recoveries after mass extinctions to events such as the Cambrian radiation of animals. In doing so, evolutionary biologists have arguably subsumed a much richer variety of processes within a single model (Erwin, '92).

The origin and diversification of grasses provides a telling example. Grasses (Poaceae) are today dominant components of many savannah ecosystems and have diversified into a variety of morphologies, including some trees (bamboos). Grasses evolved by 55 Ma (and possibly earlier) and quickly diversified into major different subclades. But, as Stromberg has shown using phytolith evidence, they were ecologically insignificant in North America (where the best data is available) until sometime in the Miocene (Stromberg, 2005). Similar macroevolutionary lags have been documented in the radiation of early insects (Labandeira, 2006) and early angiosperms (Wing et al., '92), among other clades. Thus, neither the origin of the clade nor the establishment of the major subclades was sufficient to insure the ecological success of the group. Phylogenetic diversification is not a proxy for ecological impact.

Opportunity and Adaptive Radiation

Most models of adaptive radiation posit a significant role for ecological opportunity. Two recent reviews confirm the importance of ecological opportunity but reveal little consensus on the mechanisms through which opportunity acts to promote diversification (Losos, 2010; Yoder et al., 2010). Indeed, Losos (2010) calls for greater emphasis on methods to calibrate opportunity as an important step in analyzing adaptive radiations. It is nonetheless clear that in these models, adaptive radiations occur because of preexisting ecological and evolutionary opportunities. In this scenario, the impact of evolutionary innovations may be marginal, perhaps by changing selective values sufficiently to allow greater diversification. Thus, to the extent that developmentally driven innovations are associated with adaptive radiations, it is likely to be fortuitous: an ecological opportunity exists and innovations occur, which are able to take advantage of the opportunities. One explanation for the many cases in which clades have failed to radiate despite the apparent existence of sufficient opportunity is that developmental innovations have not occurred to exploit the ecological opportunities. This is not an argument that developmental changes do not play a significant role in adaptive radiations. Studies of the beak evolution in Darwin's finches (Abzhanov et al., 2004, 2006) and wing patterning of butterflies (Brakefield and French, '99; Saenko et al., 2008) are but two examples of the importance of such changes, but not all adaptive radiations have a macroevolutionary impact.

Self-Propagating Radiations

Based on an earlier work of mine (Erwin, 2008), Losos recognized another class of evolutionary radiations, which he terms "self-propagating radiations" (I wish I had thought of the term). Losos argues that there is no clear evidence for such radiations; but I disagree, and suggest that the involvement of the niche-constructing and ecosystem engineering activities of organisms may create positive feedback situations where diversification does bootstrap higher diversity, and where specific developmental inventions may directly precipitate ecological innovation.

Certain activities of organisms can actively modify the physical and chemical environment to increase the fitness of that species or of other species. Niche constructing activities commonly produce "ecological inheritance" in the form of a physically or chemically modified environment (Dawkins, '82; Odling-Smee et al., 2003; Laland and Sterelny, 2006; Erwin, 2008). Beaver dams are perhaps the iconic example of niche construction. The environmental modifications generated by niche construction change the fitness values of the constructing organism, and thus their evolutionary trajectory. Niche construction overlaps with ecosystem engineering (Jones et al., '97; Wright and Jones, 2006), although the latter is less concerned with the evolutionary effects than the former. Ecosystem engineering is also concerned with nontrophic organismal modifications to the physical and chemical environment. It is now clear that such activities of organisms have had a major impact on ecological systems and quite probably on evolution as well, although this remains to be conclusively demonstrated. The important issue here is that the feedbacks associated with the various types of ecological facilitation can create ecological spillovers, in which the activities of one organism substantially influence the environment of other species, either positively or negatively.

Focusing on the positive interactions, these ecological spillovers can construct new environments for other species. On a larger scale, the advent of oxygenic photosynthesis eventually generated a complete change in the redox state of the Earth from anoxic and euxinic oceans and atmosphere to the well-ventilated systems we have today, and in the process facilitating the generation of far greater biomass and biodiversity than would have otherwise been possible. Similarly, the appearance of sponges during the Cryogenian and Ediacaran and advent of burrowing in the early Cambrian changed the redox state of marine waters and shallow marine sediments, respectively, and encouraged the growth of primary producers and arguably spurred the ongoing diversification of early animals (Erwin and Tweedt, 2011; Erwin and Valentine, 2012). Filter-feeding organisms can have a similar effect on oxygenation of marine waters. For example, on a more regional scale, before the advent of overfishing in the Chesapeake Bay, the American Oyster (*Crassostrea virginica*) and menhaden (*Brevoortia tyrannus*) provided critical control of the oxygen levels within the estuary, removing organic particulates and allowing high primary productivity and mesoplankton diversity and abundant fish stocks. Decimation of oysters and menhaden has converted the Chesapeake to an ecosystem dominated by jellyfish, ctenophores, pelagic microbes, and particulate organics (Jackson, 2001). These examples are all cases in which specific adaptations within clades (oxygenic photosynthesis within cyanobacteria, filtering by sponges and a coelom among some bilaterian metazoans, and particular gill types among oysters) transformed redox gradients.

What we do not learn from these examples is whether there is a tight linkage between developmental innovations and the generation of ecologically significant innovations, particularly those with spillovers, and thus in a sense whether the possibility exists of *developmentally driven* self-propagating diversifications.

INNOVATION FOR "CARRYING CAPACITY"

Of those evolutionary innovations which become ecologically widespread, some subset will have an impact on biodiversity, either species abundance or diversity. Heuristically, the easiest way to approach this is through the concept of a carrying capacity, an idea that originated in population biology through the observation of resource limitation and density dependence and the application of models of logistic growth. With finite resources, a carrying capacity represents the maximum population size. The concept of a carrying capacity applies to a population, and even with fixed resources, the number of species that can utilize a body of resources is a function of the adaptations of the species, their abundances, etc. Even assuming resource limitation for a population within a restricted area, it does not necessarily follow that the concept of a "carrying capacity" applies to a species, and certainly not to an ecological community, where the sum of positive and negative interactions between and among species produces a much more complex relationship (Monte-Luna et al., 2004). Add time, and despite discussion of "carrying capacities" over macroevolutionary time (Sepkoski, '84; Alroy, 2010), there is no particular reason why one should expect that "carrying capacities" apply on these time scales. Rather, although the maximum biomass is limited by resource availability, the distribution of species across the available resources is a function of a variety of environmental, ecologic, and evolutionary factors. Consequently, even if one stipulates that a global carrying capacity may exist on November 1, 2010, it is likely to change within a week, a month, or several years. The concept of an evolutionary "carrying capacity" is tied to long-outmoded equilibrial views of biodiversity. Despite these limitations, the concept persists and can be at least heuristically useful for phrasing one of the most interesting questions in eco-evolutionary dynamics: *how* do "carrying capacities" increase over evolutionary time? Is this a result of purely physical processes, such as warm environments and abundant shallow tropical seas, or do biological processes play an important role as well?

Although geologic changes in the physical environment (latitudinal climate gradients, increased nutrients owing to weathering, changes in ocean redox, etc.) can *create* the conditions for increased biodiversity, they do not in and of themselves generate the evolutionary novelties that result in increased biodiversity. The intriguing question is the extent to which developmental innovations increase carrying capacity or, more generally, do evolutionary innovations drive not just changes in the composition of biodiversity, but in the levels and nature of biodiversity? Are there specific sorts of evolutionary

innovation that are more likely to generate these sorts of transformative changes in biodiversity?

I believe the answers to these questions are all affirmative, and it is those developmental innovations that generate ecological spillovers through ecosystem engineering and related forms of positive ecological facilitation that drive increases in biodiversity. This means that to understand the impact of evolutionary inventions they must be considered within an ecological context. As a general example, it is unlikely that the advent of the developmental tools to form mesoderm in early bilaterians could have been identified a priori as the sort of innovation that was likely to be particularly generative for bilaterian diversity. However, once it appeared, mesoderm permitted many different clades to form a variety of coelomic spaces, a hydrocoel, and eventually vertical burrowing through sediment. This, in turn, changed sediment redox gradients, increased primary productivity, and had other ecological and evolutionary spillovers. Thus, there are likely to be specific sorts of developmental *inventions* that are likely to be generative for significant ecological *innovation*. The difficulty, I think, is that it may be quite difficult to identify ecological significance from the evolutionary invention itself. Indeed, the grass example presented earlier and macroevolutionary lags, in general, reveal the importance of contingency in ecological success. In the case of North American grasses, it was a climatic shift associated with the formation of the Rocky Mountains that evidently generated the environmental conditions that allowed the proliferation of grasslands and the attendant diversification of grassland ecosystems.

Two key points fall out from these examples: First, the pattern of novelty can be driven by the developmental inventions, the new morphologies. In some cases, as with the evolution of coelomic spaces, the morphologic invention may be sufficient. But, absent the appropriate ecological and environmental conditions, the grass example indicates that innovation may not occur. Second, ecological spillovers may generate complex patterns of feedback, increasing the diversity and abundance of organisms far removed from the original developmental invention or novelty.

Are these innovations the same as "key innovations?" Although this is an obvious question, there is no obvious answer for two reasons. First, the concept of key innovation is by now so loaded with conceptual rubbish as to be essentially useless. Key innovations are notoriously difficult to test empirically, and in many cases have devolved into whatever part of an organism an investigator has been studying. (Note that this is a methodological rather than a substantive criticism. The concept could be meaningful, but it would have to be applied with considerably more rigor than is usually the case.) Second, in an overwhelming number of cases, key innovations have been related to increases in species or taxic diversity, not ecological impact. As discussed earlier, there is no necessary connection between the two. Consequently, the rather wooly concept of key innovation is

essentially divorced from evolutionary novelties that impact carrying capacity.

CONCLUSION

Studies of evolutionary innovation have emphasized the generation of variation, and particularly the important problem of whether changes to the structure of developmental processes are a generator of evolutionary novelties. Yet, there is no reason, a priori, to expect that new developmental innovations will necessarily lead to ecologic or evolutionary success. Indeed, such as most variation, the expectation is that most developmental innovations will fail. The implicit assumption has been that, I believe, new developmental innovation will succeed or fail in much the same way as any other evolutionary change. We now have several examples of developmental mechanisms that alter their likelihood of fixation, including changes in transcription factors within developmental GRNs and the role of population size and drift in the establishment of new species, something that is particularly likely in the early stages of evolutionary diversification. More importantly, I have argued that there are certain classes of evolutionary innovations, specifically those that generate ecological spillover effects that are most likely to allow the construction of new ecological opportunities, and thus generate what Losos (2010) termed "self-propagating" evolutionary radiations. An important challenge for the study of evolutionary innovation is to develop a more nuanced view of various types of developmental changes and their probabilities of success. It is quite possible, for example, to expect studies of developmental GRNs in which the probabilities of different types of evolutionary changes and their likelihood of success can be expressed across the network.

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