

A public goods approach to major evolutionary innovations

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ABSTRACT

The history of life is marked by a small number of major transitions, whether viewed from a genetic, ecological, or geological perspective. Specialists from various disciplines have focused on the packaging of information to generate new evolutionary individuals, on the expansion of ecological opportunity, or the abiotic drivers of environmental change to which organisms respond as the major drivers of these episodes. But the critical issue for understanding these major evolutionary transitions (METs) lies in the interactions between environmental, ecologic, and genetic change. Here, I propose that public goods may serve as one currency of such interactions: biological products that are non-excludable and non-rivalrous. Such biological public goods may be involved in either the generation of new evolutionary variation, as with genetic sequences that are easily transferred between different microbial lineages, or in the construction of new ecological niches, as with the progressive oxygenation of the oceans and atmosphere. Attention to public goods emphasizes the processes by which organisms actively construct their own evolutionary opportunities. Such public goods may have facilitated some METs.

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INTRODUCTION

The major evolutionary transitions (henceforth METs) in the history of life are relatively few in number, but they serve as a curious Rorschach test for evolutionary biologists: Geneticists see them as driven by changes in the packaging and flow of information, developmental biologists by the growth of novel genes and the construction of new developmental networks, ecologists as generated by ecological opportunity, and geologists by geological processes and physical changes in the environment. These differences reflect distinct viewpoints about the relationship between evolutionary events and the changing environment and indeed about the direction of causality in some of the most fundamental changes in Earth history. Depending on which major transition is under consideration, each viewpoint may contain elements of the truth, but a more interesting question involves the interactions between these different dimensions of evolutionary innovation.

In this contribution, I characterize approaches to the METs, including alternatives to the canonical view initially developed by Maynard Smith & Szathmáry (1995), with particular reference to how these have been applied to

events during the first 3 billion years of Earth history. I then develop an approach to these transitions around the concept of public goods and suggest that this may serve to integrate the disparate views of METs into a more coherent research program.

THE CANONICAL VIEW OF MAJOR EVOLUTIONARY TRANSITIONS

Maynard Smith and Szathmáry (1995) identified seven METs each of which changed how the evolutionary process itself operated. During each transition, what had been independent evolutionary units became incorporated in a larger entity and could reproduce only as part of that larger unit, a new evolutionary individual (Table 1). For example, during the origin of eukaryotes, envelopment of a α -proteobacterium generated the symbiotic mitochondria, while endosymbiosis of a cyanobacteria produced a photosynthetic cell with a chloroplast. Each transition is also characterized by an increase in the division of labor through specialization among different components of the new unit and by changes in the nature and transmission of information. For most of these transitions (all but the second and the last listed on Table 1), the emergence of cooperation

Table 1 Canonical major evolutionary transitions, listing the original entities which become incorporated in new evolutionary individuals

From	To
Replicating molecules	Chromosomes
RNA as gene and enzyme	DNA + protein (genetic code)
Prokaryotes	Eukaryotes (packaging DNA into nucleus)
Asexual clones	Sexual populations
Protists	Differentiated multicellular organisms (plants, animals, and fungi)
Solitary individuals	Colonies (non-reproductive castes)
Primate societies	Human societies (language)

between previously independent entities required mechanisms of cooperation as well as mechanisms to suppress conflict between formerly independent units (Buss, 1987; Maynard Smith & Szathmáry, 1995; Michod & Roze, 2000). To many of those studying METs, they are also evolutionary transitions in individuality. Ågren (2014) has suggested that the process of evolutionary transitions in individuality involves three steps: the formation of a social group, the development of mechanisms to maintain the group, followed by the transformation of the social group to a new level of individuality. Surprisingly, however, the focus of Ågren's paper is not human social systems but the dynamics of transposable elements within genomes. Nonetheless, the basic framework advocated by Ågren seems applicable to multiple METs.

The early studies by Buss and Maynard Smith and Szathmáry have generated studies by a diverse array of biologists, philosophers, and even anthropologists [summarized by papers in Calcott & Sterelny (2011)]. As the discussion of the issues raised by METs has broadened, not surprisingly concerns have been raised about how widely the concept may be applied (Herron *et al.*, 2013). In general, however, the focus of this avenue of research has been on information transfer as a key to the METs, whether it is via the packaging of genetic information into new evolutionary units, or adjustments to manage potential conflicts between formerly independent entities. What is particularly striking to a geologist is how little attention has been paid to either the ecological or environmental context in which these transitions occur [(Knoll & Hewitt, 2011) being a notable exception].

PLANETARY DRIVERS AND MAJOR EVOLUTIONARY TRANSITIONS

Geologists and geochemists have tended toward more environmentally based explanations for METs, generally identifying abiotic changes in tectonics, sedimentation, climate, and redox as the planetary drivers of discontinuous evolutionary change. Advocates of this perspective tend to view biotic evolution as passively responsive to changes in the physical environment. This large class of

explanations includes work linking climate and evolution (Vrba, 1993; Gienapp *et al.*, 2008; Valentine *et al.*, 2008; Erwin, 2009), tectonics and evolution (Stanley & Hardie, 1999; Peters, 2005), and redox changes such as anoxic events or increased oxygen levels (Knoll, 2003; Johnston *et al.*, 2012).

A first-order class of planetary drivers would include the putative late heavy bombardment [3.9 billion years ago (Ga)], and some later large impact events such as that at the end of the Cretaceous; redox changes associated with the great oxidation event (GOE) about 3.4 Ga and the late Ediacaran–Cambrian transition (c. 600–540 Ma) (Anbar & Knoll, 2002) as well major global glaciations in the Palaeo- and Neoproterozoic (Kirshvink, 1992; Hoffman *et al.*, 1998). Changes in chemical cycles would include the end of mass-independent fractionation of sulfur and its association with changes in oxygen levels (Farquhar *et al.*, 2000; Guo *et al.*, 2009) and the shift in the locus of silica formation from nearshore in the Proterozoic to offshore by the late Phanerozoic (Maliva *et al.*, 1989). Focusing on the Archean and Proterozoic, Van Kranendonk (personal communication, 2012) identified six events where geologic processes might have driven biological change. These included the transition to modern tectonics (3.2 Ga), the emergence of continents and changes in sulfur isotopes (3.0 Ga), massive volcanic outgassing of CO₂ and SO₂ (2.8 Ga), the rise of atmospheric oxygen, linked to granite/greenstone formation about 2.7 Ga, the formation of banded iron formations, the earliest Phanerozoic glaciations and the end of mass-independent sulfur fractionation (2.3 Ga), and the global magmatism, generation of black shales, and the Lomagundi carbon isotope event (2.2 Ga), which could be linked to the origin of eukaryotes (see also Lyons *et al.*, 2014).

While some of these changes, such as climate change, are cyclical, many of the most interesting major evolutionary and geological events involve unidirectional non-uniformitarian transitions in the dynamics of Earth processes. In other words, as with many historical events, the transition has changed the state space of the processes involved such that some events are now precluded, but other events become possible. An interesting avenue for further exploration is the evolutionary impact of cyclical or recurrent vs. non-uniformitarian planetary drivers. METs are inherently non-uniformitarian (as recognized by Maynard Smith and Szathmáry), as are some ecological changes. Changes in atmospheric redox appear to have involved a change in the state space for the Earth's environment, and this is reflected in geochemical patterns linked to redox (mass-independent sulfur fractionation, etc).

In van Kranendonk's argument, cycles of geologic and tectonic change led to increases in oxygen level and facilitated evolutionary responses. Yet, there is little doubt that the rise of oxygen involved complex feedbacks between

biological innovations and changes in the physical environment (Reinhard *et al.*, 2013; Knoll & Sperling, 2014; Lenton *et al.*, 2014; Lyons *et al.*, 2014; Planavsky, 2014). While the origin of oxygen and its importance in facilitating biotic evolution has been discussed for decades, yet it is less clear whether the accumulation of atmospheric and oceanic oxygen during the GOE and during the Neoproterozoic was a purely geologic process or involved biological facilitation (compare Lyons *et al.*, 2014 with Lenton *et al.*, 2014, for example).

The diverse environmental changes of the late Archean and Paleoproterozoic serve as a counter point to the relative tectonic and environmental stability of the Meso- and Neoproterozoic. Christened the ‘boring billion’ by Holland (2006), the persistent stability of this interval had long been apparent to geologists. A suite of environmental and tectonic indicators from about 1.7 Ga to 800–750 Ma indicate a prolonged interval of tectonic stability associated with the stable supercontinental configurations of Nuna and Rodinia (Roberts, 2013; Cawood & Hawkesworth, 2014). This was a time of extensive early eukaryotic diversification, including the advent of numerous multicellular lineages (Knoll *et al.*, 2006; Knoll, 2011), and the evolutionary dynamism was much less than during the intervals on either side.

The planetary driver view of METs is conceptually similar to the invocation of ecological opportunity as a motivating force in adaptive radiation, as discussed in the following section. Although METs differ in many ways from classic adaptive radiations, planetary drivers may provide new resources or create ecological opportunities for diversification. They are also analogous to ‘market-pull’ models of economic growth in which an unmet need within an economic market creates an opportunity that leads in turn to a response that fills the need. The planetary driver model, however, views biological evolution as an essentially passive response to environmental forces. In contrast, much recent work in ecology and evolutionary biology addresses the ways in which many organisms actively manipulate their own environment, over both the short and the long term (Odling-Smee *et al.*, 2003; Wright & Jones, 2006; Wilkinson *et al.*, 2009; Gibling & Davies, 2012), as discussed further below. Few studies of METs have examined the extent of biological facilitation [but see Tziperman *et al.* (2011) for one such example].

EXPANDING ECOSPACE AND MAJOR EVOLUTIONARY TRANSITIONS

Ecological interactions were missing from the view of METs articulated by Maynard Smith and Szathmáry, but this deficiency was addressed by Knoll and Bambach (2000) who identified six significant expansions (megatrajectories) in ecospace: the origin of prebiotic metabolism, the metabolic diversification of bacteria and archaea, the

origin and expansion of unicellular eukaryotes, the diversification of aquatic multicellular clades, the invasion of land, and the origin of intelligence. Although several of these overlap with METs as defined by Maynard Smith and Szathmáry, Knoll and Bambach focused on expansion of ecospace utilization and the means of gathering resources. They link such increased ecospace utilization to a directional pattern of increased ecological complexity through the history of life and thus embed their work within broader discussions over the role of contingency and determinism (Erwin, 2015). Knoll and Bambach emphasized that although each phase requires and builds upon the preceding, attaining one level did not imply when or if a succeeding level would appear. Thus, each level was contingent, and there is no deterministic pattern of progress toward greater ecological complexity.

The views of Knoll and Bambach build on a long tradition in paleontology and evolutionary biology of invoking new adaptive and evolutionary opportunities as a driving force in evolutionary change. Simpson’s view of macroevolutionary change largely revolved around expansion of lineages into new adaptive zones (Simpson, 1944, 1953). For Simpson, adaptive opportunities could be expressed as a suite of hierarchically nested zones and subzones that may evolve over time, representing a ‘characteristic reaction and mutual relationship between environment and organism, a way of life and not a place where life is led’ (Simpson, 1953, pp. 201–202). This view of evolution as a ‘space’ into which evolution could adapt a species or clade influenced many subsequent paleontologists and evolutionary biologists. Simpson distinguished the progressive occupation of adaptive zones from an adaptive radiation, the essentially simultaneous divergence of lineages from a single ancestral type, a model that Simpson applied from a radiation of bird species to the Cambrian radiation. The view that ecological opportunity fuels evolutionary diversification was further elaborated by Mayr (1960, 1963) and continues in many current views (Schluter, 2000; Losos, 2010; Yoder *et al.*, 2010).

PUBLIC GOODS AND MAJOR EVOLUTIONARY TRANSITIONS

Public goods are characterized by the use of the good by one actor not excluding the use of the good by others (non-excludability) and by the inability to prevent others from using the good (non-rivalry). The most obvious examples of public goods in economics are linked to information, such as the calculus: There is no limit to the number of integrals that can be solved at the same time. A closely related concept is that of a club good, such as a GPS signal, where the signal is non-rivalrous but highly excludable (by encoding the signal); tollways, social societies, and clubs are other examples of goods where

barriers to use can be erected even when the good is non-rivalrous. Economic theories on the factors that facilitate or promote growth are wonderfully diverse and debate continues over the relative importance of technology, education, population growth, and other factors. Here, however, I wish to use concepts from endogenous growth theory focusing on the importance of public good in driving innovation (on endogenous growth theory and public goods, see Jones, 2002; Romer, 1990). Although the concept of public and club goods was developed in economics, organisms generate a diverse array of public and club goods (Erwin, 2008; McInerney *et al.*, 2011; Erwin & Valentine, 2013) and the concept is increasingly being used in evolutionary biology. The theory of public goods has been widely used in discussions of the evolution of cooperation, particularly in microbial systems. For example, Bachmann *et al.* (2013) described the role of public vs private goods for metabolic strategies of cells in culture. Levin (2014) discussed the application of public goods to social evolution, while Dobata and Tsuji (2013) applied public goods theory to asexual ant societies. Here, however, I want to focus on the potential role of public goods during METS that occurred during the Archean and Proterozoic and suggest that specific public goods were associated with these transitions. Focusing on biological goods is rare in discussions of METs, but provides a currency linking differing viewpoints.

As will become apparent in the following discussion but is worth emphasizing, public goods may impact two different aspects of the process of evolutionary innovation: by facilitating the generation of variation upon which selection and drift can act, or by constructing evolutionary opportunities (often viewed as new niches) required for the success of novel phenotypes. Since Mayr's paper on evolutionary novelty (Mayr, 1960), most evolutionary biologists have, like Mayr, viewed evolution as inherently opportunistic: 'Useful' evolutionary adaptations will quickly become taxonomically diverse or ecologically successful. Those that are not useful, as judged by the environment, will disappear. In other words, in contrast to the standing variation upon which natural selection can act at the population level, there is no standing body of evolutionary novelties awaiting appropriate conditions to expand. Except that Mayr was wrong. Macroevolutionary lags, long delays between the origin of a clade and its eventual taxonomic or ecologic success, are not uncommon and may be more widespread than generally appreciated. Examples include the origin and later spread of grasses (Stromberg, 2011), the spread of angiosperms (Wing *et al.*, 1992), and the origins of metazoan orders (Jablonski & Bottjer, 1990). These lags emphasize that any general model of evolutionary novelty must give as much attention to the success of novelties as their origin (Erwin & Valentine, 2013), and public goods may play a role in both ends of this process.

A recent study of the genomes of 61 different individuals of *Escherichia coli* found that although a predicted 15 741 gene families are found across all 61 sequences (most individuals have 4000–5500 genes), only 6% of genes are found in every individual. Thus, some 80% of the genes in a typical genome are 'accessory' genes (Lukjancenko *et al.*, 2010). This is one example of the emerging fluidity of many genomes (see discussion in Koonin (2012)) that serves as the foundation for the most explicit application of public goods to evolution (McInerney *et al.*, 2011). The ubiquity of horizontal or lateral gene transfer between often distantly related lineages creates substantial difficulties for those favoring a strictly tree-like pattern in the history of life. McInerney and colleagues argue that many nucleotide sequences are best seen as public goods, with individual sequences recruited by microbial lineages as needed. Just as in economics, public biological goods are those where the acquisition and use of the good by one organism does not preclude its use by another organism, even one in a phylogenetically very distant clade. In the view of McInerney and colleagues, much of genomic innovation involves gene acquisition and recombination in which microbes share a large suite of easily accessible genes (Dagan & Martin, 2009). In microbial associations or syntrophies, where diverse lineages form obligate communities, gene distribution may be restricted to members of the community and thus form club goods (McInerney *et al.*, 2011). (It would be interesting to learn whether a genomics approach to modern stromatolites would reveal gene distributions consistent with a club goods interpretation). Gene sequences as public goods may have played an important role in several major events in the history of life, including the origin of cells at the origin of life and the origin of the photosynthetic chloroplast within eukaryotes.

There are two leading and competing views on the origin of life: a metabolism-first view, invoking the primacy of energy-gathering metabolism, and an information-centric view, concerned with the development of a stable information transmitting machinery, now largely focused on the RNA world hypothesis. There is an enormous and often contradictory theoretical and experimental literature addressing these issues, far beyond the scope of this contribution to address. Rather, I want to highlight a potential resolution to this debate first mooted by Woese (1998, pp. 6854), when he suggested that organismal lineages as such did not exist early in the history of life, but rather there was 'a diverse community of cells that survives and evolves as a biological unit'. Woese visualized a communal ancestor that underwent progressive 'annealing' to crystallize into distinct lineages. The earliest components to crystallize, such as the translation machinery, became public goods (as described here), broadly utilized by elements of this community. This hypothesis has been widely discussed, with Glandsdorff *et al.* (2008) perhaps representing a maximally

complex last universal common ancestor as a community of shared attributes. One implication of this view, clearly recognized by Woese and elaborated by other workers (e.g. Dagan & Martin, 2009), is that networks often better capture the complexity phylogenetic relationships in different gene families than do trees. Widespread lateral gene transfer among microbial lineages highlights the continuing role of gene sequences as public goods.

As sequences form public goods, particularly during the origin of life, so do genes subject to lateral gene transfer serve as public goods during subsequent microbial evolution. Lateral gene transfer among all three domains of life has turned out to be sufficiently widespread that there have been many concerns about the ability to reliably reconstruct phylogenetic relationships across the history of life (Rivera & Lake, 2004; Choi & Kim, 2007; Keeling & Palmer, 2008; McInerney *et al.*, 2011).

The origin of eukaryotes, probably sometime after 1.8 Ga, involved the development of stable endosymbiosis and thus cells rather than gene sequences became a new form of public good, albeit one that was easily transformed into a club good, restricted to a single clade. Fossil evidence for this transition remains contested, in part because there are few identifiable characters of stem-group eukaryotes (Knoll, 2014). Symbiotic relationships are characteristic of eukaryotes and have enabled a wide range of primary, secondary, and tertiary endosymbiosis. The symbiotic origin of chloroplasts from a cyanobacterium and the mitochondria, likely from a α -proteobacteria, are the best-known examples of eukaryotic symbiosis (Katz, 2012). There is an ongoing debate about the extent to which other primary components of the eukaryotic cell may reflect symbiotic events. The eukaryotic nucleus is clearly a chimera of both archaeal and bacterial genes, but the implications of this for the phylogenetic foundations of eukaryotes remain unclear (Katz, 2012; Koonin & Yutin, 2014; McInerney *et al.*, 2014). Most evidence suggests that the formation of the mitochondrion was a singular evolutionary event, although it is less clear whether this is also true of chloroplasts. My focus here, however, is not on the origins of eukaryotes, but rather on the role of symbionts as public goods in expanding the metabolic and ecologic repertoires of eukaryotes. For example, whatever the origin of plastids, it is clear that they have been transferred to many different lineages via secondary and even tertiary engulfment of chloroplast-containing eukaryotes (Delwiche & Palmer, 1997; Keeling, 2013). In a recent paper, Douglas highlights two important types of symbiotic interactions: (i) the provision of novel metabolic capabilities for the eukaryotic host and (ii) increased fitness through physiologic benefits of the symbiont (Douglas, 2014). Both interactions are widespread across eukaryotes and suggest that these secondary and tertiary symbioses render eukaryotes functionally multicellular. Although research in this area remains limited, a plausible interpretation is that much

of the metabolic and physiologic diversity of bacteria and archaea (albeit mostly the former) serves as a reservoir of public goods for eukaryotic evolution.

The role of genes as public goods focuses on their involvement in generating new variants for evolutionary change. But public goods also appear to be involved in generating new evolutionary opportunities (as well as destroying evolutionary opportunities for other clades). Two events, the origin of oxygenic photosynthesis and the eventual GOE and the origin of multicellularity, and particularly the origin of animals, illustrate the potential of public goods to create new evolutionary opportunities in addition to altering the nature of genetic variation.

The evolution of photosystem II and oxygenic photosynthesis generated oxygen as a waste product. Although the initial redox changes in the oceans may have been small and localized, the cumulative effect of the spread of oxygenic photosynthesis was a change in the redox state of the shallow oceans, leading to the GOE about 2.4 Ga and an increase in atmospheric oxygen (Blank & Sanchez-Baracaldo, 2009; Sessions *et al.*, 2009; Lyons *et al.*, 2014; Planavsky, 2014). Although these changes doubtless had a negative impact on many anaerobic taxa, the construction of an increasingly aerobic environment created new niches for other organisms. A beaver dam is a classic example of this process, for while creating a habitat for a family of beavers, the dam building modifies the surrounding habitat for many other species. This is an example of what is variously called niche construction (Odling-Smee *et al.*, 2003; Laland & Boogert, 2008) and ecosystem engineering (Jones *et al.*, 1997; Cuddington *et al.*, 2007). Niche construction and ecosystem engineering are conceptually similar, addressing the modifications that organisms make to their environment and the effects of these modifications on biodiversity. Niche construction focuses more on the fitness effects of these modifications, making it more difficult to follow in the fossil record (Erwin, 2008). The most generative effects of niche construction occur when these activities spillover to impact the fitness and evolutionary dynamics of other species. Thus, the net effect of the onset of oxygenic photosynthesis was the generation of new evolutionary opportunities, not only for the diversification of cyanobacteria, but also for many other lineages ecologically linked to them, or to the oxygenic environment they constructed. Moreover, oxygen is perhaps the pre-eminent example of a biological public good. As mentioned, it is a waste product of cyanobacteria and is difficult for other organisms to monopolize. Thus, once oxygen begins to build-up in the oceans and atmosphere, it is available to any organisms that choose to utilize it for oxygenic metabolism. The effects of these opportunities are also recorded in an expansion of gene families, tied to a relatively rapid Archean diversification (David & Alm, 2011). Approximately 27% of modern gene families arose at this time, and

most of these gene families are associated with electron transport and respiratory pathways. Niche construction/ecosystem engineering does not generally produce public goods, but when they are formed, it may be highly generative of biodiversity.

Erwin and others have recently proposed that the Ediacaran–Cambrian diversification of metazoans (largely, although not exclusively, of bilaterians) also involved a major contribution of ecosystem engineering activity through the biologically mediated ventilation of the oceans through the carbon sequestering action of sponges, and the bioturbation of shallow marine sediments by burrowing organisms (Erwin & Tweedt, 2011; Erwin *et al.*, 2011; Erwin & Valentine, 2013). Here, oxygen also acts as a public good mediating the expansion of biodiversity. Experimental studies of modern systems have shown that bioturbation changes redox gradients in sediments, increases primary productivity, and enhances biodiversity (Lohrer *et al.*, 2004). The onset of vertical, penetrating bioturbation near the Ediacaran–Cambrian boundary leads to the demise of microbially bound sediments and an increase in well-mixed sediments through the first several stages of the Cambrian. This biologically mediated ventilation of marine sediments was (and continues to be) a public good that benefits the burrowing organisms but also many other species. More recently, Alegado & King (2014) have suggested that the transfer of bacterial sequences to animals may have played a role in early metazoan diversification.

The argument here is that many, and perhaps most, of the METS involved the origin and spread of public goods. The spread of these public goods in many cases involved ecological spillovers that constructed new niches for other taxa, providing positive feedback for increased diversity.

DISCUSSION

The canonical view of METs, as well as those favored by some paleontologists and others common to geologists, focuses on different aspects of these evolutionary transitions. The Maynard Smith and Szathmary view ignores the ecological and environmental context of METs, while the ecological perspective of Knoll and Bambach is relatively silent on the mechanisms undergirding their expansion of ecospace and downplays contributions from genetics and development. The environmental focus of the planetary driver models favored by some geologists relies upon temporal correlation rather than specific mechanisms and also views organisms as passively responding to environmental change.

Moving forward with understanding the causes and consequences of these events requires a more integrated approach, incorporating genetic, environmental, and ecological information, and the feedbacks between them. In this contribution, I have argued that biological public goods may have played an important role as a currency

linking the three domains of this macroevolutionary triad. Public goods may act both to change the nature of the available variation upon which evolution can act, as well as to expand evolutionary niches.

Although the focus of this paper has been on the role of public goods during METs, it should be obvious that similar public good may play a role in other circumstances. For example, type IV secretion amidase effector proteins are very effective antibacterials and have been transferred at least six times into various eukaryotic lineages, including at least twice among animals (Chou *et al.*, 2015). Similarly, molecular evidence suggests that the ability to form a siliceous skeleton has been acquired by several different eukaryotic groups through lateral gene transfer of silicon transporter-type genes (Marron *et al.*, 2013).

As originally recognized by Maynard Smith & Szathmary (1995), the METs also pose a challenge for evolutionary theory, as all of the explanations discussed here are inherently non-uniformitarian (Erwin & Davidson, 2009; Erwin, 2011). What I mean by this is that the nature of evolutionary change has itself evolved over time, with the creation of new sources of variation, new evolutionary individuals, and new levels at which selection can operate. Traditional evolutionary theory, somewhat oddly for an inherently historical discipline, is uniformitarian in the sense that it does not include the possibility that the range of variation or selection may change directionally over time. The non-uniformitarian nature of evolutionary change has both positive and negative aspects. While many of these changes may expand the range of evolutionary responses, as has been the case with most of the METs as defined by Maynard Smith and Szathmary, other changes canalize evolutionary responses. As Davidson and I discussed, the hierarchical structure of developmental gene regulatory networks within animals features recursively wired regulatory circuits that control regional patterning of the developing embryo (Davidson & Erwin (2006, 2009)). The formation of these circuits appears to have stabilized this aspect of developmental patterning, but largely forced subsequent evolutionary changes upstream or downstream of these kernels. This permanently altered the types of developmental variation available for selection. Similarly, the METs discussed here, whether viewed from an information perspective, as the result of planetary drivers or as a consequence of the expansion of ecological complexity were similarly non-uniformitarian. One aspect of this evolution of the evolutionary process has been the introduction of new sorts of public biological goods (Erwin, 2015).

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