

Ecological drivers of the Ediacaran-Cambrian diversification of Metazoa

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Abstract Organismal modifications to their physical and chemical environment play a significant role in structuring many modern ecosystems, and experimental evidence suggests that such behavior can increase diversity. Despite the important role such activities play in connecting ecology and evolution, less is known of the macroevolutionary impact of such influences, especially their role during major evolutionary transitions. The Ediacaran-Cambrian diversification of Metazoa encompassed the appearance and early diversification of virtually all major clades of marine animals and the establishment of metazoan-dominated ecosystems. Here we assess the role of positive ecological feedbacks using a new compilation of the first occurrences of all metazoan phyla, classes; orders and equivalent stem taxa, as well as data from a previously published compendium on fossils from the early to middle Cambrian of China. The results reveal relatively minor feedback during the Ediacaran, but a substantial increase during the Cambrian, principally through bioturbation and the appearance of a number of structural engineers, including sponges. Chemical modification of the environment through filtering and bioturbation seems to have had the largest impact. Data on taxic diversity is a poor proxy for abundance, or for the actual environmental impact of these activities, however. Future assessments of the influence of ecological feedbacks on this event will require standardized assessments of the abundance of taxa with different ecological roles.

Keywords Ediacaran · Cambrian · Ecology · Feedback · Niche construction

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Introduction

In 1607 oysters (*Crassostrea virginica*) covered the shallow surfaces of the Chesapeake Bay (eastern United States) to a depth of about 9 m and large oyster reefs were a hazard to navigation. Yet by the end of the twentieth Century oysters had almost disappeared, largely as a consequence of overfishing and pollution along the rivers leading into the Chesapeake. Today the ecology of the Bay has changed, perhaps irreparably, from an ecosystem with extensive benthic and pelagic primary productivity, high mesozooplankton density and abundant fish stocks, to one dominated by jellyfish, ctenophores, pelagic microbes, and particulate organic carbon (Jackson 2001; Newell 1988, 2004; Ulanowicz and Tuttle 1992).

The loss of the American oyster has played a significant part in this ecological shift. Oysters are active filter feeders, removing suspended organic matter and inorganic particles $<3 \mu$. By one estimate, during the mid-1800s oysters filtered all the waters of the bay above 9 m in 2½–4 days, and the entire bay in some 3–6 days. Major harvesting of oysters began by the 1870s, and by 1988 the equivalent filtering required an estimated 244 and 325 days, respectively. Based on the estimated carbon demand and phytoplankton productivity, the pre-1870s biomass probably removed 23–41% of total phytoplankton carbon production (Newell 1988). Today the few remaining oysters have little effect on the water quality of the Bay. Oysters, like many filter-feeding bivalves, package their waste products into excreted pellets or pseudofeces which in turn transfer nitrogen and phosphorus from the phytoplankton to benthic ecosystems (Newell 1988). Such coupling between pelagic and benthic ecosystems increases with bivalves that have high clearance rates and that eject a large number of particles (Newell 2004; Ostroumov 2005). Thus, oysters significantly modified both their physical and chemical environment, in so doing, modified the environment for all other species in the bay.

The effect of oysters in the Chesapeake Bay is a microcosm for how species can influence their physical and chemical environment. Other marine clades with similar filter-feeding effects include sponges, other bivalves, vermetid gastropods, polychaete worms, ascidians, barnacles, fish and even bryozoans (Dame et al. 2001). The magnitude of the effect depends on such variables as the water residence time (turnover from outside the system), the rate of primary productivity and the clearance time (the time required for filter-feeders to filter the water of the ecosystem, which is in turn a function of the biomass of filter-feeders, particle concentration rates, temperature and other variables) (Dame and Prins 1998). In undisturbed modern ecosystems filter-feeders can have a substantial impact on water quality.

Although, there has been considerable work over the past two decades on the ecological and microevolutionary aspects of ecological facilitation, niche construction and ecosystem engineering, their macroecological and macroevolutionary effects have not been widely explored (Erwin 2008). Ecosystem engineering has a variety of definitions, but an useful one is: *modifications to the abiotic environment by a species that affects resource availability for another species* (Jones et al. 1997; Wright and Jones 2006). Ecosystem engineering may create, modify or destroy the niches of other species, and thus influence their evolution, but the focus has largely been on ecological impacts rather than evolutionary processes (Erwin 2008). Species that engage in ecosystem engineering are known to interact non-linearly, generating positive feedbacks that enhance diversity (Altieri et al. 2010).

In the case of the American oyster, filter-feeding is a trophic activity and not a component of ecosystem engineering, but filtering and oxygenating the waters of the Chesapeake are chemical effects, as is delivering nutrient-rich waste products to the sediment.

Buildups of shell mounds are a physical effect. In this case both the chemical and physical processes have a positive influence on oysters, but they also have spillover effects, both positive and negative, on a host of other species in the Bay. These influences are both ecological, affecting the environment and consequently both the presence or absence as well as diversity of species, but also evolutionary. Persistent ecological modifications form a sort of ecological inheritance, influencing the environment, and thus the fitness, of other species as well as themselves independent of genetic inheritance (Laland et al. 1999; Laland and Sterelny 2006; Odling-Smee et al. 2003). These evolutionary effects are often described as niche construction: the informed activities of organisms that influence their environment and affect the fitness of the population (Odling-Smee et al. 2003). Objects with ecological inheritance transfer information from one generation to the next, but outside the organism and independently of the genome (Fig. 1). This dynamic can set up a strong pattern of eco-evolutionary feedback through habitat modification, nutrient and carbon cycling and related effects (Post and Palkovacs 2009).

Here we are concerned with the reverse of the Chesapeake oyster story: not the loss of ecological feedback, particularly ecosystem engineering, but rather its origin during the initial diversification of animals in the Ediacaran (635–542 million years ago [Ma]) and Cambrian (542–490 Ma) periods. Specifically: What was the role of ecological and evolutionary feedback during the Ediacaran and Cambrian radiations? In particular, does such activity enable or drive what Losos (2010) has termed ‘self-propagating’ adaptive radiations? The evolutionary effects of ecosystem engineering may have helped drive the Ediacaran-Cambrian diversification, but exploring this hypothesis requires translating our knowledge of the ecological dynamics of settings such as the Chesapeake into a macro-evolutionary perspective.

Here we evaluate the different degrees of chemical and physical modification during the Ediacaran-Cambrian diversification through a new compilation of the timing of origination of metazoan clades as well as a compilation of generic diversity for the early Cambrian of

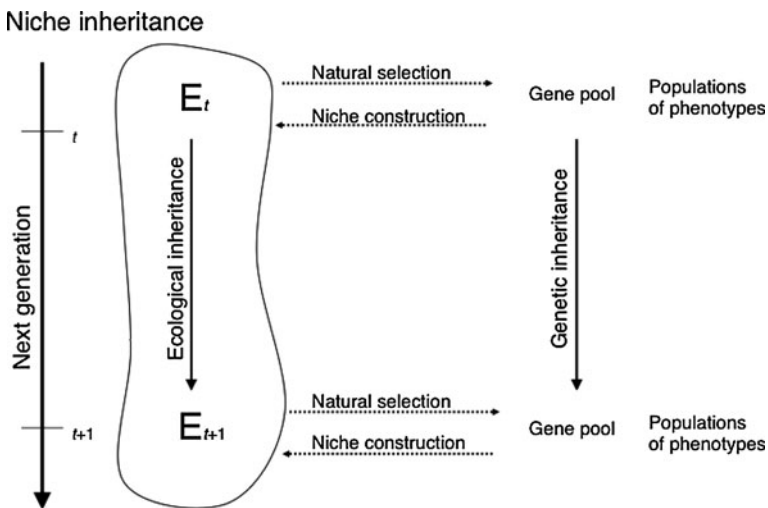


Fig. 1 Niche construction involves the production of external phenotypes that may persist in the environment, as an ecological inheritance, and affect selection on subsequent generations of the species. The consequences of niche construction thus modify the selective environment of the species. From a figure by J. Odling-Smee

South China. Although the currently available data is limited, we argue that such modifications in the pre-Ediacaran were limited to microbial trapping and binding of sediment and their geochemical effects, particularly on sedimentary redox, and the sediment baffling effects of algae. Ecological feedbacks played a successively more important role during the Cambrian and Ordovician in facilitating the overall growth of diversity. We conclude by suggesting future directions for this aspect of evolutionary ecological research.

Ediacaran-Cambrian diversifications

The origins and early diversification of most major clades of marine animals occurred during a great period of evolutionary innovation between about 635 and 510 Ma (Bengtson 2005; Chen 2009; Erwin 2005; Erwin et al. submitted; Erwin and Valentine 2012; Knoll and Carroll 1999). During this time the geochemistry of marine environments was very different from today. Geochemical evidence demonstrates that the oceans were anoxic, and probably iron and sulfur-rich before 600 Ma (Halverson et al. 2009). The transition to a more oxygenated ocean took place fitfully between about 600 and about 555 Ma (Schields-Zhou and Och 2011). Oxygenation of the oceans was a necessary condition for large animals because of the energetic advantages (Catling et al. 2005), and it is likely that animal diversification was at least partly constrained by oxygen levels. Molecular clock evidence indicates that crown group demosponges and cnidarians were both present about 700 Ma (Erwin et al. submitted), while the earliest fossil evidence comes from sponge biomarkers (preserved fossil molecules) dating to older than 635 Ma (Love et al. 2009) and possible sponge body fossils (Maloof et al. 2010b). There is little evidence for animal body fossils until after 579 Ma, when the peculiar soft-bodied organisms of the Ediacara macrofauna first appear in Newfoundland (Narbonne 2005; Xiao and Laflamme 2008). A variety of fronds, quilted benthic forms and other morphologies have been discovered, but few were capable of any movement, and only one, *Kimberella*, which appears after 555 Ma, shows any evidence of a mouth or a gut (Fedonkin et al. 2007). The Ediacara macrofauna flourished until 542 Ma. For decades paleontologists placed these organisms within various Phanerozoic (<542 Ma) bilaterian clades, but there is now general agreement that they are not easily associated with extant metazoan groups. The most reasonable interpretation of their phylogenetic affinities is that they represent a variety of metazoan clades lying above sponges, and below the origin of the protostomes and deuterostomes (Davidson and Erwin 2010; Erwin 2009; Laflamme et al. 2009; Sperling and Vinther 2010; Xiao and Laflamme 2008). This makes interpreting the feeding behavior of Ediacaran organisms rather challenging. Surface-area/volume ratios and morphology suggest that at least some of these organisms were osmotrophic, feeding off dissolved organic carbon in seawater (Laflamme et al. 2009), while others likely digested the abundant microbial mats that bound much of the shallow sea bottom before the evolution of grazing and burrowing animals.

The bulk of the first appearances of bilaterian metazoan clades occur between about 530–520 Ma and mark one of the most profound intervals of morphologic innovation in the history of life. This Cambrian Explosion includes the first appearance of virtually all of the major clades of metazoans, including a large number of stem group molluscs, lophophorates, arthropods and others. The Cambrian radiation established assemblages dominated by arthropods, inarticulate brachiopods, hyolithids and a few other taxa.

There are dozens of ‘explanations’ for the Ediacaran-Cambrian diversification of animals, some of which emphasize the importance of environmental changes, others

developmental innovations, while another class focuses on the growth of new ecological relationships. The events of the Ediacaran and Cambrian involved all three of these factors, and it is fruitless to debate the relative merits of each. The ecological mechanisms occur within a complex milieu, and a full understanding requires integration across a broad range of disciplines Erwin and Valentine (2012).

Data and methods

No comprehensive database exists of the pattern of Ediacaran-Cambrian originations. Most reports that have depicted the patterns of origination or diversity (Knoll and Carroll 1999; Marshall 2006) used data from Sepkoski's family and generic compendia, but this dates from the mid-1990s (Sepkoski 1992, 2002). To understand ecological feedbacks the most appropriate data would be locality-based records in which the variety of feedbacks could be scored, and for which the Paleobiological Database project (<http://www.Paleodb.org>) would be useful. Although the PBDB was not designed to collect the first and last occurrences of taxa, the locality-based approach will eventually prove valuable in analyzing the significance of ecosystem engineering during the early Paleozoic. However, the Ediacaran and Cambrian records in the database needs to be populated with far more localities and with better stratigraphic precision before such studies can be undertaken.

There is, however, a significant and persistent bias in relying on locality data to analyze these ecological properties. Paleontologists largely work with the record of organisms with durably skeletonized hard parts: shells, carapaces, bones, etc. We miss the abundance and ecological significance of lineages lacking a durable skeleton. However, during the Cambrian we have the Chengjiang and the Burgess Shale faunas, the best known of more than a dozen extraordinarily well-preserved assemblages of early and middle Cambrian age. Together, these assemblages document the diversity of many lineages whose Cambrian importance would otherwise be unknown. In addition, the fossil record of the earliest Cambrian (Stages 2 and 3) is dominated by a diverse assemblage of minute shells, tubes, scales and other elements, collectively described as the 'small shelly fauna' (SSF). Many of these fossils have been preserved with phosphate replacing the original carbonate. This phosphatization was a product of the unusual ocean chemistry of the time, so the SSF are, in their way, just as extraordinary as the Burgess Fauna (Malloof et al. 2010a). In short, during the Cambrian we have a far richer record of the overall diversity of lineages that would otherwise not be readily preserved, but different types of preservation are found at different localities, and some clades are known from only a small number of sites. This in turn limits the utility of locality-based analyses.

As a preliminary step in assessing the possible role of ecosystem engineers in the Ediacaran-Cambrian diversification, we employ two different databases. First, in mid-2009 DHE began compiling data on first occurrences and diversity of Ediacaran and lower to middle Cambrian fossils, focusing on the first appearances of phyla, classes, orders and equivalent stem groups. Although identifying higher Linnean taxa was relatively straightforward in the mid-1980s (Erwin et al. 1987), the rise of phylogenetic systematics has resulted in the recognition of a large number of stem-lineages, a particularly acute problem in the Cambrian, and the distribution of recognized stem lineages is also non-random with respect to clades. The systematics is updated based on the most recent analyses for each group. The stratigraphy is based on the new international standards for the Cambrian (Babcock and Peng 2007; Zhu et al. 2009). Other details of the data

compilation and the version of the data used in this paper have been published elsewhere (Erwin 2011; Erwin et al. [submitted](#)).

The second database is a generic compendium of ranges of all marine metazoa from the early Cambrian of South China, including the Chengjiang biota (Li et al. 2007). This encompasses 876 named genera, of which Li et al. consider 582 to be valid. We updated the stratigraphy, converted the compilation to the new Cambrian stages and tabulated the stratigraphic ranges of all valid genera within major groups through the first four stages of the Cambrian (Table 2).

Having established the origins of each clade, and their approximate generic diversity during the early Cambrian of China, we then classified their modes of modifying the environment. Within the literature on ecosystem engineering there has long been a debate over whether a process- or outcome-based approach is more appropriate, with most favoring a process-based approach. For example, Jones (Jones et al. 1994) distinguished between autogenic and allogenic engineers, (Gutierrez et al. 2003) recognized flow modifiers, habitat modifiers and biogeochemical modifiers, and (Cuddington et al. 2009) discussed obligate and non-obligate engineers, as examples of the range of proposed classifications. Other papers have adopted other classifications, specific to each study. Although most work on ecosystem engineering has focused on physical modifications of the environment (Jones et al. 1994), Jones explicitly included chemical effects as well, although they have received less attention.

Here we are concerned with the functional effects of engineering, and so distinguish a suite of modifications of the physical or chemical environment. Relevant activities during the Ediacaran-Cambrian include physical ecosystem engineering, encompassing: (1) structural or architectural activities (building structures), (2) sediment bioturbation and bulldozing; and (3) sediment stabilization. Relevant aspects of chemical engineering include: (1) oxygenation and ventilation of the water column or sediment; and (2) nutrient transfer. Although, this classification was developed for the events of the Ediacaran and Cambrian, it closely matches the functional classes independently articulated by Berke (2010): structural engineers (encompassing both reef constructors and sediment stabilization), bioturbators, light engineers and chemical engineers. Each of the clades known as fossils from the Ediacaran and Cambrian was assessed for ecosystem engineering activities based on their structure, functional morphology, and where relevant, ecology of living relatives (Tables 1 and 2).

Structural modification includes the formation of reefs by microbes (as stromatolites and thrombolites) during the Neoproterozoic and by archaeocyathid sponges during the early-mid Cambrian. (Reefs date back to about 2 billion years ago and have been constructed by a variety of organisms since then; reefs constructed by corals are a relatively recent phenomenon). Sediment stabilization by microbial mats is widespread during the Ediacaran (Hagadorn and Bottjer 1997), but declines during the early stages of the Cambrian (Bottjer et al. 2000). Some of the large, recumbent Ediacara fauna, such as the rangeomorphs, may have also produced local sediment stabilization, but the effect would have been much less than from the more widespread microbial mats. Sediment bulldozing and burrowing is a type of physical alteration of the environment but the *effects* are both physical (changing the physical properties of the sediment) and chemical (changing the redox conditions within the sediment) (Lohrer et al. 2004; Mermillod-Blondin and Rosenberg 2006; Nogaro et al. 2009). Horizontal bulldozing was limited during the Ediacaran, with the bilaterian *Kimberella* responsible for horizontal grazing traces in microbial mats (Fedonkin et al. 2007; Ivantsov 2009). During the Cambrian the extensive increase in both horizontal and vertical burrowing progressively produced a well-churned sediment

Table 1 Types of physical and chemical ecosystem engineering types and effects for the principle Ediacaran and Cambrian engineering clades, as discussed in the text

Clade	Physical ecosystem engineering			Chemical ecosystem engineering	
	Structural	Bulldozing	Sediment stabilization	Ventilation	Nutrient transfer
Ediacaran					
Microbial mats			X		
Organic buildups	X				
Rangeomorphs		X			
<i>Kimberella</i>		X		X	
Sponges	X				X
Cambrian					
Sponges	x			x	x
Archaeocyathids	x			x	
Chancellorids	x			x	
Brachiopods				x	x
Phoronids		x		x	
Priapulids and annellids	x		x		
Trilobites		x		x	

(Jensen et al. 2005; Seilacher et al. 2005), ventilating the sediments and increasing microbial primary productivity. During the early Cambrian the principal bioturbators were a variety of worms, including priapulids and phoronids; annelids, although important today, do not appear to have been ecologically significant during the Cambrian. Some arthropod groups would have contributed as well, although diverse arthropod assemblages did not appear until well into the early Cambrian, and thus were not involved in the Cambrian Explosion.

Chemical engineering creates biogeochemical gradients and includes nutrient and carbon transfer between different components of an ecosystem, ventilation or oxygenation of the water column, and ventilation of the sediments. Biogenic mixing of water bodies, even in the open ocean, by planktonic and nektonic organisms can be significant (Breitburg et al. 2010). Zooplankton and early metazoans likely caused the first biogenic mixing in the Cambrian but the overall impact during the Cambrian is likely to have been minimal. A more significant source of biogenic mixing during the Ediacaran and the Cambrian is the effect of pumping by sponges. Ventilation of the water column and the sediments would have been enhanced during the Cambrian by a variety of sponges, including the heavily calcified archaeocyathids, as well as by chancellorids (probably sponge-like), inarticulate brachiopods and various bioturbators.

Other forms of ecosystem engineering may have occurred during this interval, but their impact is difficult to assess. Plankton functioned as light engineers, altering light intensity and penetration and affecting the carbon cycle (Butterfield 1997), but are not considered here. Predation and relocation have been considered as components of niche construction (e.g. Odling-Smee et al. 2003; Post and Palkovacs 2009) but are not considered here because they do increase habitat heterogeneity and thus diversity.

Table 2 Summary data from Li et al. (2007) with the generic diversity of different Cambrian clades, by stage

Clade	Stage 1 eMeis	Stage 2 m/l Meis	Stage 3 qiong/catl	Stage 4 longw
Sponges (non archaeocyath)		5	24	
Archaeocyathids			33	
Cnidarians	3	8	8	3
Ctenophora			4	
Annelids			2	
Hyalolithids	5	23	27	2
Helcionellids		34	10	1
Misc mollusca		35	3	1
Chancelloirids		3	3	1
Brachiopods		12	8	3
Phoronids			2	
Sipunculans			2	
Priapulids and other worms			20	
Chaetognath			1	
Protoconodonts	1	4	4	
Lobopodians			8	
Anomalocarids			3	
Bradoriids			34	
Trilobites			113	54
Other arthropods			51	
Echinoderms			2	1
Vetulicolians/chordates			12	
Enigmatic chengjiang metazoans			19	
Enigmatic tubular fossils	1	18	7	
Enigmatic sclerites	1	27	11	0
Total	11	169	421	66
SSF	11	164	65	11
As % total fauna	100	97	15	17
% Trilobites	0	0	27	82
# Ecosystem engineers		24	76	4
% Ecosystem engineers		14	18	7

Li's compiled the data based on Chinese stages, but for easier comparison to Table 1 these were converted to International Cambrian Stages (Stages 1–4). The primary ecosystem engineers are shown in bold. As many trilobites also disturbed the sediment, as did some of the 'other arthropods' this underestimates the actual diversity of ecosystem engineers. The figure summarizes the numbers and percent of small shelly fossils (SSF), percentage of trilobites per stage, and the number and percent of ecosystem engineers. Other abbreviations: *eMeis* Early meishucunian, *m/l meis*: middle to late meishucunian, *qiong/catl* qiongzhusian, and *canglangpuan*, *longw* longwangmiaoan

Results

Few of the Ediacara macrofossil groups appear to have generated significant modification to either the physical or chemical environment. Stabilization of the sediment by microbial

mats (Gehling and Droser 2009) may have been the most significant form of Ediacaran ecosystem engineering, followed by the ventilation and carbon transfer effects of sponges (Sperling et al. 2007). The total impact of sponges on the ecosystem remains unclear however, although, on molecular evidence sponges originated well before the Ediacaran, it has been difficult to unambiguously identify Ediacaran-age sponge fossils and their abundance is unknown (Sperling et al. 2011). The role of sponges is considered separately below. Among the Ediacara macrobiota, some rangeomorphs would have had localized abilities to stabilize the sediment, particularly such non-frondlike forms as *Fractofusus*. Some dickinsoniids may have had a similar impact, although it would have been much less than the cumulative effect of microbial mats. Similarly, the holdfasts of the many frond-like Ediacaran forms may have locally stabilized sediment. In contrast, the apparent microbial grazing of *Kimberella*, and the osmotrophy of *Yorgia* and related forms (Lafamme et al. 2009) would have reduced microbial mat integrity. Thus, the likely effects of Ediacaran ecosystem engineering appear to have been primarily some sediment stabilization and the nutrient transfer effects of sponges.

The number of clades that include active ecosystem engineers expanded considerably during the first several stages of the Cambrian. These include sponges, including archaeocyathids and possibly chancellorids, as well as inarticulate brachiopods, phoronids, priapulids and annelid worms, and trilobites. Structural engineers became more common. Cambrian reefs were largely built by sponges, particularly the well-skeletonized archaeocyathids. Archaeocyathid reefs were locally abundant during the early stages of the Cambrian and could have generated important regional engineering effects, but they disappeared in the middle Cambrian. Overall, reefs were relatively insignificant compared to reefs later in the Paleozoic (Kiessling 2008). Bulldozing and bioturbation also increased, with planar laminated sediments essentially disappearing as nearshore marine sediments became well mixed by burrowing organisms. These activities expanded chemical ecosystem engineering. As a proportion of total diversity the recorded Cambrian fossil record was dominated by small shelly fossils in Stages 2 and 3, and by various arthropod clades during the remainder of the Cambrian. Many arthropods, including trilobites had little if any ecosystem engineering effects, but some of the larger predatory forms may have had an impact through bioturbation.

The greatest engineering effects were likely to have come from sponges, however, in a manner very similar to the oysters described in the introduction. Sponges can filter large volumes of water and as they remove bacteria they can also release minute eukaryotes as well as bioactive metabolites and dissolved inorganic nitrogen (Diaz and Rutzler 2001; Reiswig 1971). The estimated capture rates for sponges are 29–1,970 mg Cm⁻² d⁻¹, comparable to that for oysters (573 mg Cm⁻² d⁻¹) (Gill and Coma 1998). Large sponges can filter their volume in about 5 s (Vogel 1977). Some of the flow through sponges does not require active pumping, but is a simple consequence of water flow over the osculum by ambient currents (Vogel 1977). In addition, sponges are essentially large sacks of collagen, so depending on burial efficiency, their death also results in a net transfer of carbon from the water column to the sediments, achieving a similar end result that oysters achieve through deposition of pseudofeces. By removing carbon, even at low oxygen levels, sponges can potentially have enormous spillover effects on the geochemistry of marine waters.

In the absence of detailed information on the relative importance of these effects at specific localities through this interval these results are necessarily limited. Data on first occurrences and generic diversity provides little insight into the critical issue of the relative abundance of different engineers, nor can they reveal possible positive feedbacks on the

diversity of other groups. Despite these limitations, however, the results are sufficiently informative to suggest the need for more intensive field investigations.

Discussion

The evidence from metazoan clades and trace fossils during the early Cambrian supports the conclusion that a significant increase in ecosystem engineering was associated with the explosion of bilaterian metazoan clades at this time. But was the expansion of ecosystem engineering merely a component of the establishment of metazoan-dominated marine ecosystems, or was it a significant driver of this event? We cannot definitively resolve this question with the data presented here, but the evidence is suggestive that the ecological expansion was driven, at least in part, by ecosystem engineering. This may best be understood by comparing the events of the Ediacaran-Cambrian with classic models of adaptive radiation.

The Ediacaran-Cambrian differs substantially from a classic adaptive radiation in morphologic breadth, in involving a large number of different clades, rather than one, and in the construction of metazoan ecosystems, rather than diversification within the framework of an existing ecosystem (Erwin 1992). A classic adaptive radiation reflects the exploitation of an ecological opportunity presented by underutilized resources (Losos 2010; Schluter 2000; Simpson 1953; Yoder et al. 2010). These opportunities could involve the appearance of new resources, liberating resources through extinction of previous occupants, colonization of a region where resources were under-utilized, or evolution of a trait that permits utilization of resources in a new way (Losos 2010; Simpson 1953). The last of these corresponds to cases where a ‘key innovation’ has been identified that is generative and opens new evolutionary possibilities. From the perspective of the organism, the last three are special cases of the appearance of new resources.

In the simple case of an adaptive radiation on an island, an initially generalized species may become subdivided into a suite of more specialized species, with the number of new species depending on the resources available. Thus, total abundance may be the same, simply distributed across a greater number of species. More commonly, however, we might expect that specialization will also allow a species to more effectively acquire resources, so that the total abundance of all members of the component populations after an adaptive radiation will be higher than at the outset with a single, generalized species. Since ‘carrying capacity’ was originally a population level concept (although it has subsequently been extended to species, communities and even to the global ecosystem), this amounts to an increase in carrying capacity. The limit, of course, is imposed by available resources. The interesting adaptations are those that allow the acquisition of new or previously unexploited resources.

The classic view of adaptive radiation requires an exogenous source of ecological opportunity to drive the diversification. Some evolutionary diversifications may involve positive feedback, such that an ongoing diversification may generate its own ecological opportunities, bootstrapping diversity to higher levels than would otherwise been the case (Erwin 2007, 2008). Losos (2010) described this as a ‘self-propagating’ adaptive radiation, and suggested that it could occur either through species evolving to exploit other species within a diversifying clade, or, as DHE had earlier suggested, through ecosystem engineering. Losos accepted that such cases could occur, but noted that few had been documented.

Ecosystem engineering is a broader concept than niche construction because it can encompass a variety of activities that do not necessarily impact the organisms that produce them. Often a variety of different species, in some cases belonging to different phyla, may contribute. In these cases, the situation is somewhat different than diagrammed in Fig. 1. The ecological inheritance still exists, but the effects may *spill over* to impact the ecological and evolutionary success of other species (Fig. 2). It is the generation of these spillovers that produces effects on other species, and on the ecosystem as a whole.

The Ediacaran-Cambrian and perhaps also the Ordovician radiation appear to represent situations in which ecosystem engineering spillovers have driven self-propagating diversifications, and the polyphyletic nature of these two events may explain why few have previously been identified. Classic adaptive radiations involve a single clade, and often (although not always) relatively restricted trophic breadth. We suggest that the driving force behind self-propagating radiations is the generation of ecological spillovers (Fig. 2) between groups at different trophic levels. Specifically, a particular class of organismal engineering activities increases the availability of resources to organisms in the community. Diversifications that generate ecological spillovers with broad environmental effects are most likely to have such generative consequences. The filter-feeding activity of sponges during the Ediacaran, and their putative impact on the global carbon cycle and on oxygenation of marine waters, illustrates an ecological spillover from ecosystem engineering that greatly enhanced potential diversity by changing ocean redox, much as the Chesapeake oysters affected that estuary. These ecosystem engineers construct ecological and evolutionary opportunities both for their own clade, and for many others.

Indeed the extent of ecological spillovers during the Cambrian considerably exceeds what is suggested by the diversity approach presented here. This compilation does not capture the substantial increase in bioturbation during the early Cambrian. Trace fossils in the Ediacaran are largely limited to simple, relatively unspecialized horizontal traces that

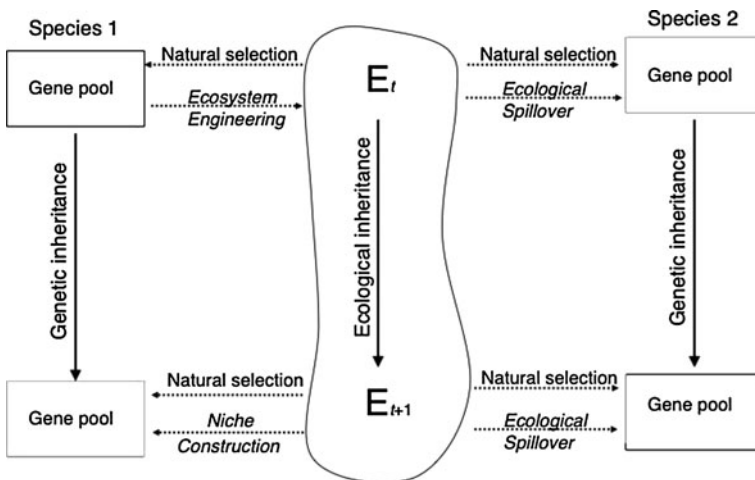


Fig. 2 A schematic of the relationships between genetic and ecological inheritance during ecosystem engineering, based on Fig. 1. The ecosystem engineering activities of species 1 modify the environment of the species, generating immediate ecological spillover for species 2, as well as ecological inheritance that may modify selection for species 1 (niche construction *sensu stricto*) and ecological spillover to effect, in a future generation, selection on species 2

do not penetrate into the sediment and thus have little effect on sediment chemistry, although they may have influenced the chemistry of microbial mats. In contrast, Cambrian trace fossils are larger, have greater structural complexity and many penetrated into the sediment (Jensen et al. 2005, 2006). The net result of the increasing number of clades burrowing through the sediment was a decline and eventually an elimination of the microbially-bound substrates of the Ediacaran and an increase in more heavily bioturbated sediments, which has been described as the ‘Cambrian substrate revolution’ (Bottjer et al. 2000; Seilacher and Pflüger 1994). This transition occurred over perhaps 20 million years, and resulted in ventilation of the sediments, and a change in redox gradients. However, although ecosystem engineering was responsible for the ventilation of the water column and shallow sediments during the first several stages of the Cambrian, this is reflected in neither the first occurrence records nor the generic diversity data.

Katija and Dabari (2009), working with jellyfish, show that viscosity-enhanced biogenic mixing can have a substantial impact on ocean mixing, particularly when large numbers of organisms are swimming together. While jellyfish were likely present throughout the Ediacaran and Cambrian, assessing their abundance and thus engineering effects is difficult. (Swimming organisms that school are likely to induce greater biogenic mixing than single organisms, where friction will dampen the effects, and the evolution of sharks, bony fish, marine reptiles and finally marine mammals could have played a progressively more important role in keeping the oceans mixed later in the Phanerozoic). Today zooplankton and fish contribute about equally to biogenic mixing and have been estimated provide energy roughly equivalent to wind and tides (Dewar et al. 2006).

Although, ecosystem engineering expanded considerably from the Ediacaran into the Cambrian, the number of clades engaged in such activities was far fewer than later in the Phanerozoic. This raises two possibilities, neither of which can be satisfactorily tested with diversity data alone. The first possibility is that although the diversity of ecosystem engineers was limited, they were sufficiently abundant to generate significant environmental effects, just as the single species of Chesapeake oyster provides no indication of the magnitude of their impact on the Bay. Alternatively, the major innovations in ecosystem engineering may have happened later, particularly during the Ordovician radiation, which saw a spectacular rise in metazoan diversity, the origin or expansion of many of the major Paleozoic clades, and the establishment of the Paleozoic Evolutionary fauna which dominated marine communities until the end-Permian mass extinction (Sepkoski 1995; Servais et al. 2010; Webby et al. 2004). During that episode, the trilobite-dominated benthic marine assemblages of the Cambrian and Early Ordovician were displaced by new communities of suspension-feeding articulate brachiopods, bryozoans and stalked echinoderms; mobile and predatory groups were less common. By the end of the Ordovician there was extensive epifaunal tiering and a marked change in reef composition from microbially-dominated buildups to metazoan-dominated reefs. The diversity of phytoplankton appears to have increased considerably, leading to the development of a diverse zooplankton and an expansion of pelagic organisms.

Although investigation of the effects of ecosystem engineering associated with the Ordovician radiation is beyond this paper, there are indications that it may have been extensive. Table 3 documents the diversity of different clades during the Ordovician and notes the physical and chemical ecosystem engineers. Compared with Tables 1 and 2 the number of clades involved in both physical and chemical ecosystem engineering increased, with particularly marked increases in structural or architectural engineering, as reflected by the resurgence in metazoan-dominated reefs, as well as in the number of clades whose activities ventilated either the water column or the sediments (through bulldozing). As with

Table 3 Ordovician fossil groups, with their generic diversity and associated ecosystem engineering effects

Clade	Number of genera	Physical ecosystem engineering			Chemical ecosystem engineering	
		Structural	Bulldozing	Sediment stabilization	Ventilation	Nutrient transfer
Sponges	135	X				X
Stromatoporoids	29	X			X	
Conularids	12			X		
Corals	128	X			X	
Bryozoans	169	X		X	X	
Inarticulate Brachiopods	190				X	X
Articulate Brachiopods	540	X		X	X	X
Polyplacophoran molluscs	15					
Symmetrical univalves	75					
Gastropods	140		X			
Bivalves	136		X		X	
Rostroconchs	21					
Nautiolid cephalopods	305					
Hyalolithids	32					
Scolecodonts (polychaete jaws)	50		X		X	
Chaetognaths	4					
Paleoscolecidans	8					
Machaeidians	7					
Trilobites	842		X		X	
Eurypterids	6					
Ostracodes	559					
Phyllocarid crustaceans	9					
Echinoderms	431			X		
Chitinozoans	35					
Graptolites	192					
Conodonts	106					
Vertebrates	35					
Receptaculitids	9	x				

See text for discussion of types of engineering. Diversity is for the entire Ordovician, and most clades listed here expanded considerably in diversity during the Middle and Late Ordovician. Diversity is from (Webby 2004) based on the papers in (Webby et al. 2004)

the Cambrian radiation, there was a considerable expansion of infaunal burrowing associated with the Ordovician radiation, including new forms of burrowing, and more intensive bioturbation (Droser and Bottjer 1989; Mangano and Buatois 2007).

Encompassing events from Galapagos finches to the Cambrian Explosion as an adaptive radiation provides little insight into the diversity of processes or consequences involved. Many ecosystem models suffer from a number of problems in addressing the generation of diversity: (1) Few capture the effects of niche construction and ecosystem engineering,

particularly the spillover effects that may ripple through an ecosystem [see (Krakauer et al. 2009) for an exception]. Some adaptations are far more consequential than others, something that can be modeled by varying the contribution of different species to diversity. (2) Carrying capacity is usually an exogenous variable, rather than an endogenous variable that reflects interactions with other model variables. (3) The carrying capacity does not change overtime during a model run or simulation. This makes it difficult to explore the effect different parameter values may have on ‘carrying capacity’.

Caveats

Several commentators have excluded assimilatory and dissimilatory activities from ecosystem engineering (Jones and Gutierrez 2007). Such a definition of ecosystem engineering would exclude a number of processes that have been studied as ecosystem engineering, particularly changes in the chemical environment. As Berke (2010) notes in her detailed analysis of the issue, this produces logically flawed conclusions, where passive production of chemical gradients does represent ecosystem engineering, but active transport is excluded as ecosystem engineering, even if the chemical outcome is identical. In the specific case of sponges, active pumping by sponges would be excluded but passive flow (which occurs in many sponges) would count as ecosystem engineering. It is obviously impossible to determine whether, and when, fossil sponges engaged in active or passive flow. Since the issue is the analysis of the ecological and evolutionary effects of organismal activities, rather than some sort of ideological purity, we have followed the general trend in the field and the analysis of Berke, and include such activities as ecosystem engineering.

Summary

Although the degree of ecosystem engineering associated with Ediacaran ecosystems appears to have been relatively small, sponges may have had a cumulative impact on ventilating the oceans by removing organic material from the water column. Ecosystem engineering expanded considerably during the first several stages of the Cambrian, particularly as bioturbation ventilated the sediment and archaeocyathid sponges provided increased habitat complexity. Although detailed studies are needed, the major pulse of Paleozoic ecosystem engineering may have developed during the advent of the Paleozoic Evolutionary Fauna during the Ordovician radiation. All of these conclusions are limited, because they are based on the first appearance and generic diversity patterns of various clades, rather than ecological abundance. The impact of ecosystem engineers depends on abundance, however, which is infrequently assessed by paleontologists. Further understanding the macroevolutionary implications of ecosystem engineering will also require more robust eco-evolutionary models that better account for niche construction and ecosystem engineering, and particularly for the spillover effects that may influence other taxa.

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