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Review

Ecosystem engineering, regime shifts and the rise of animals

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SUMMARY

The term ‘ecosystem engineering’ refers to biotic processes that modulate the availability of resources to other species. These processes thus modify, maintain or create habitats and impact the abundance and diversity of species within ecosystems. In turn, the study of ecosystem engineering in the fossil record is leading to a re-evaluation of the influence of organisms on the deep-time evolution of Earth-system structure and function. With this comes a growing recognition that biological forces may be key drivers of major transitions in Earth history. There are two crucial questions: first, have new ecosystem engineering processes emerged randomly throughout geologic time, or are they clustered? Second, to what extent has their emergence driven episodes of evolutionary radiation or extinction? Here, we address these questions through the lens of the Ediacaran–Cambrian transition (~575–530 million years ago) — an interval that witnessed the rapid rise of animals, following nearly four billion years of microbial dominance. We propose that an engineering regime shift occurred in the late Ediacaran that gave rise to new rules of community assembly, new ecological niches, and altered macroevolutionary trajectories. We argue that the recognition of ecosystem engineering regime shifts may help us not only to understand other key intervals in the Phanerozoic, but also to project the future of ecosystems under human influence.

Introduction

The present-day structure and function of the Earth system is the result of over four billion years of cumulative bioengineering, with life influencing habitability on a wide range of temporal and spatial scales, and thus also profoundly influencing macroevolutionary patterns. Understanding when, and especially how, the evolution of new biotic processes has led to major Earth-system shifts offers a chance to understand

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Figure 1. Benthic ecosystem engineers in the modern ocean and their early evolutionary counterparts from the Ediacaran–Cambrian transition.
Recent work hypothesizes that the emergence of these processes drove dynamic macroevolutionary patterns across the Ediacaran–Cambrian transition, including pulses of both origination (i.e., as part of the Cambrian explosion) and extinction. Examples by column, from top left to bottom right: Gastropod surface trail. Polychaete (*Hediste diversicolor*). Oyster reef formed by *Neopycnodonte cochlear* (image: Max Wisshak). Seagrass meadow (*Zostera marina*; image by Sofia Sadogurska/Wikimedia Commons (CC BY 4.0)). Crinoid meadow (image by C.G. Messing/Wikimedia Commons). Scleractinian coral bioherm (image by Toby Hudson/Wikimedia Commons (CC BY-SA 3.0)). *Parapsammichnites pretzeliformis* (basal Spitskop Member, Nama Group). Unidentified *Treptichnus* isp. trace fossil (basal Spitskop Member, Nama Group). *Thectardis avalonensis* (Mistaken Point Ecological Reserve, Newfoundland). *Tribrachidium heraldicum* (SAM P12898). *Skinnera brooksi* (SAM P35629). *Ernietta plateauensis* (GSN F389). The 'Seilacher surface' (Mistaken Point Ecological Reserve, Newfound land). *In situ* archaeocyath buildup (Wilkawillina Limestone; South Australia). *Cloudina* and *Namacalathus* buildups on Farm Driedoornvlagte (Zaris Formation; Nama Group).

the coevolution of our planet's biotic and abiotic components on long timescales.

In ecology, organisms that have an outsized effect on modulating the availability of resources are called 'ecosystem engineers'. As originally defined[1], ecosystem engineers cause physical state changes in biotic or abiotic materials, and in doing so modify, maintain or create habitats. Consequently, ecosystem engineers have significant impacts on the abundance and identity of species within the ecosystem and thus community structure[2]. Subsequent work has sought to extend these concepts into an evolutionary context. For example, the term 'niche construction' describes engineering-type processes that control local to regional-scale patterns of species richness and shape evolutionary opportunity via modification of their environment[3]. Similarly, the term 'evolutionary engineers' points out that the influence of animals on ecology and the environment has given rise to evolutionary innovation, and thus the structure and composition of the present-day biosphere is 'a space designed by metazoans'[4]. Lastly, a recent framework that attempts to unite the study of biotic engineering processes in shallow and deep time distinguishes between ecosystem engineering and a new term — 'Earth-system engineering'[5]. These latter processes alter the chemical, physical or functional characteristics of the Earth, modulate resource flows on a planetary scale and have lasting impacts ('legacy effects'[6]) that can persist for millions of years. Earth-system engineering thus impacts biota that do not necessarily coexist with the engineers in space and time and can have outsized effects on macroevolutionary dynamics[6–8].

These concepts readily lend themselves to analysis through the lens of the fossil record. Biotic engineering processes can be preserved in the form of body- and trace fossils (Figure 1), while the engineering consequences to environments are reflected in a range of geochemical signatures that can be readily detectable in sediments[5,7–9]. Moreover, molecular phylogenetic datasets are providing an indirect means for reconstructing the rise of engineering processes through intervals of time where the fossil record is sparse[10] and represents an innovative means for reconstructing engineering processes beyond the reliable temporal limits of the fossil record. These fossil, geological and phylogenetic histories also present a unique opportunity not afforded by the study of modern systems alone: they allow us to establish links between engineering processes and consequences and enable detection of long-term ecological and evolutionary outcomes[5].

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Reconstructing the evolutionary history of engineering-type processes is thus becoming a key area of research in the fields of geology, paleontology and evolutionary biology, allowing us to address fundamental questions surrounding the influence of life on Earth-system structure and function, and in driving major transitions in Earth history. Two such questions are: first, have new biotic engineering processes emerged evenly throughout geologic time, or emerged in clusters during specific intervals? Second, to what extent has their emergence driven episodes of evolutionary radiation or extinction? The answers to these questions are not only important to understanding the present-day planet, but potentially also offer a roadmap for understanding the long-term consequences of anthropogenic engineering processes, which have been driving ongoing species extinction and ecosystem degradation[11].

In this review, we examine these two questions in light of the Ediacaran–Cambrian transition (~575–530 million years ago (Ma)). During this interval the first major radiation of macroscopic animal life took place, along with behaviours, physiologies and body plans associated with a wide variety of novel ecosystem engineering processes, such as bioturbation, metazoan biomineralization and the first animal reefs, that continue to play vital roles in the modern oceans (Figure 1) and helped shape the subsequent Paleozoic[12–14]. We also test a key prediction of conceptual frameworks centered on the evolution of new engineering processes, namely that increases in engineering processes should be associated with major evolutionary turnover[4,15,16]. We argue the answer to this question potentially has relevance not only for understanding other critical intervals in the Phanerozoic, but also the future of ecosystems under human influence.

Engineering the early Earth

An important question centres on how quickly organisms began engineering their environment following the origin of life. A recent study[10] reconstructs and dates the last universal common ancestor of life on Earth (LUCA) using a new phylogeny comprised of bacteria and archaea. They infer LUCA likely appeared ~4.2 billion years ago (Ga) and no later than the end of the Hadean (~4.09 Ga), a mere 300–500 million years after the formation of the moon. As important as timing is the nature of LUCA: it is hypothesized to have been a complex anaerobic acetogen whose waste acetate would have created metabolic niches for other community members, including methanogens, and supporting a modestly productive early ecosystem[10]. The earliest microbial communities were thus likely responsible for vital engineering processes, with the inference that — for almost as long as there has been life on this planet — it has influenced nutrient flows in ways that both control short-term ecological richness patterns and create longer-term evolutionary opportunity.

After the Hadean, the Archaean and Proterozoic eons saw the evolution of new microbial metabolisms and thus the progressive engineering of several major biogeochemical cycles. Microbial sulfate reduction is known from 3.47 Ga[17], while sulfur oxidation likely emerged between 2.7 and 2.4 Ga[18] and in deep-water marine settings by 2.52 Ga[19]. Oxygenic photosynthesis by cyanobacteria evolved perhaps as early as 3.2 Ga, although substantial oxygenation of the atmosphere (the Great Oxidation Event) didn't occur until ~800 million years later at around ~2.4 Ga[20,21]. The various biotic components of the nitrogen cycle emerged in step-wise fashion starting in the Archaean, with the reduction of molecular nitrogen (i.e., N-fixation) by ~3.2 Ga[22], nitrate reduction by ~2.8 Ga[23], ammonia oxidizers by ~2.1–1.9 Ga[24] and denitrifying and nitrate-metabolizing pathways by ~1.5 Ga[22]. A major step-change in planetary habitability came, however, in the aftermath of the Great Oxidation Event 2.1 Ga with the relatively quick rise in atmospheric oxygen levels to ~1–10% of present day levels[25]. The rise in oxygen led to substantial changes in the diversity of bioavailable minerals and thus the source material for a wide variety of potential nutrients[26,27]. The subsequent appearance of eukaryotes in the Proterozoic fundamentally changed the biological pump, i.e., the biological sequestration of carbon from the atmosphere, and its sequestration into deep marine sediments — representing a key shift in Earth-system engineering[4,5]. The resulting enhanced carbon export has been linked to global shifts in the carbon cycle[28] and extreme glaciation events[29]. The rise of algae is thought to have been particularly important, leading to more complex ecological dynamics[30] and new ecological niches[31].

Some of these Archean-Proterozoic engineering processes were local in scale. For example, microbial mats and stromatolites would have altered the physical state of environments, including the physical properties of sediments[32], the physical and biogeochemical nature of the sediment–water interface[33] and fluid dynamics[34]. The majority of processes, however, were predominantly chemical in nature, altering nutrient flows on global scales and thus largely qualifying as Earth-system engineering. In turn these innovations established the conditions (principally, oxygen levels[35]) required for the emergence and diversification of metazoans, thus intensifying engineering impacts on more local scales. In this sense, the successive emergence of new ecosystem and Earth-system engineering processes exerted a crucial intrinsic control on the pace and timing of emerging biological complexity. This point was recently explored in depth[25] in a re-examination of the 'hard steps' model for the emergence of intelligent life. In this revised view, biospheric evolution on Earth proceeds in a broadly deterministic fashion, governed by increasing habitat diversity, and the opening of successive 'windows of habitability' (both of which may themselves be biologically engineered)[25]. The rise of animals in the Neoproterozoic thus marks an inflection point in the history of biotic engineering[4].

The rise of animals across the Ediacaran–Cambrian transition

The Ediacaran Period (635 to <538.5 Ma) is marked at its base by the end of the Marinoan glaciation, the last of the Neoproterozoic Snowball Earth events[36], and features the earliest abundant macrofossils of putative animals at 574.17 ± 0.66 Ma in the Drook Formation of southeastern Newfoundland[37]). Fossil communities first appear in deeper water settings on the continental shelf, representing more stable environments and a physiological refuge that would have minimized oxygen stress[38,39]. Subsequently, communities migrated upslope into shallower water, with the first well-dated macrofossils from the Lamtsa Formation (White Sea area of Russia), underlying an ash bed recently re-dated to 557.28 ± 0.6 Ma[40]. These shallow water communities mark the apex of Ediacaran diversity[13,41,42], and preserve the

first definitive evidence for motility, sexual reproduction and the presence of animal phyla that would unambiguously become part of the subsequent Cambrian radiation[43–45]. The terminal Ediacaran is characterized by communities that appear transitional between those of the preceding Ediacaran and the succeeding Cambrian, with increasing numbers of taxa referrable to extant metazoan phyla. At this time, predation and biomineralization first appear along with evidence for increasing levels of niche partitioning and ecological specialization (for example, in feeding mode and habitat preference[12–14,46,47]). This fossiliferous interval of the late Ediacaran has been informally split into three assemblages: the Avalon (~574–560 Ma), White Sea (~560–550 Ma) and Nama (~550–538 Ma), which are succeeded by the base of the Cambrian Period (currently <537.65 ± 0.25 Ma[48] and potentially as young as 533 Ma[49]). The subsequent 10–25 million years records the most intense burst of metazoan diversification known from anywhere in the Phanerozoic fossil record, with the vast majority of currently extant animal phyla appearing in a geologically short period of time[49–51] and leading to the assembly of Paleozoic ecosystems.

The Ediacaran–Cambrian transition was a highly dynamic interval, characterized by multiple waves of evolutionary innovation[13], and one or more pulses of biotic turnover, which have been interpreted as extinction events[12,41,52]. Based on a new compilation of genus occurrences (Figures 2J,K, S1 and S2 and Tables S1–S3), we identify several pulses of origination of new fossil genera in the Avalon, a major pulse late in the White Sea, minor pulses in the Nama, and finally large pulses in the Cambrian. Interspersed with these are pulses of apparent extinction that contribute to drops in diversity in the late Avalon, a major drop over the White Sea–Nama transition, and smaller drops in the late Nama. Although these analyses do not account for potential sampling biases[53], they suggest a broad picture of dynamic global diversity throughout the Ediacaran and earliest Cambrian, with one substantial biotic crisis ~550 Ma, and spectacular diversification in the Fortunian (<538 to ~529 Ma).

Several abiotic, strictly environmentally driven processes have been suggested as explanations for these patterns. For example, in Nama Assemblage sediments from Namibia, there is evidence that macrofossils — and the first appearance of more complex behaviours — follow fleeting pulses of oxygenation in the basin[54,55]; more generally, there is evidence that dynamic redox conditions may help to generate evolutionary novelty[56]. There is also a possible coincidence in time between pulses of anoxia and a putative extinction event at ~548 Ma coincident with the White Sea–Nama transition[40,41]. However, to date, the evidence for this anoxic pulse has not been found outside of South China, and so it is unclear if this is a global or regional signal[52]. Meanwhile, biologically driven explanations have also been suggested, pointing to the role emerging ecosystem engineering processes may have played in creating new habitat, and in changing marine environments in ways that selected against certain lifestyles[57–61]. At least one recent study frames the extinction event at the White Sea–Nama transition as a turnover between stem- and crown-group metazoans, driven by the ecosystem engineering impacts associated with more modern-looking animal groups[52]. There are thus both abiotic and biotic models that have been invoked to explain late Ediacaran extinction events[52].

These two models are not mutually exclusive. For example, increasing levels of oxygen could have created the initial conditions required for evolutionary innovation, which in turn could have led to novel engineering processes that created new ecological and evolutionary opportunity. However, the biotic engineering model is arguably much harder to test and support, requiring the reconstruction of engineering processes, quantification of these processes (along with their downstream geobiological consequences), and then finally plausible hypotheses that link these processes with patterns of origination/extinction. We might also expect a macroevolutionary lag between the appearance of a process and the ecological and evolutionary consequences[5], requiring a highly resolved geochronology. Below, we review some recent attempts to reconstruct and quantify the rise of metazoan ecosystem engineering and discuss plausible links with macroevolutionary trends across the Ediacaran–Cambrian transition.

The rise of animal ecosystem engineering

In this section we briefly introduce each ecosystem engineering process, identify fossil groups thought to be performing it, and finally describe recent work — and outstanding questions — surrounding their hypothesized long-term macroevolutionary impacts. We begin with bioturbation, principally because traces recording the physical movement of sediment by organisms are among the best-preserved records of ecosystem engineering in the fossil record[9,59–61].

Bioturbation

In the present, bioturbators are powerful influences on biogeochemical cycles and the maintenance of infaunal habitats[62,63]. Bioturbation is often split into two processes, biomixing and bioirrigation[64], where biomixing refers to the mixing of solid sediment particles, and bioirrigation refers to the mixing of pore water solutes below the sediment–water interface. Of the two, bioirrigation is often thought to represent the more powerful process, as it more effectively introduces oxygen into the sediment, shifting redox gradients and directly controlling the availability of redox-sensitive elements. In turn, this expands habitable sediment tiers in the subsurface[65,66], and impacts the composition of microbial communities[67]. Both biomixing and bioirrigation behaviours also affect sediment rheology; sediment mixing by organisms greater than a few millimetres in length has been shown to prevent microbial mat formation[68], and — with deeper penetration depths — burrowing contributes substantially to the formation of structurally weaker substrates and increasing depth of the mixed layer[69].

The last decade has revealed that bioturbation behaviours associated with a variety of ecosystem engineering processes extend surprisingly far back into the Neoproterozoic (Figure 3). Over 20 genera of trace fossil (ichnogenera) are now known from the Ediacaran (Figure S1), with a first step-increase in diversity occurring over the White Sea–Nama transition, and a second in the earliest Cambrian. Although diversity of trace fossils and environmental impact are broadly decoupled[61,70], these new behaviours were associated with increasing burrow depth and the appearance of new engineering modes[61] (Figure 2A,B and Table S1). The key question, however, is: to what extent can the emergence of new bioturbation behaviours be linked to pulses of origination, or extinction? In some instances, this

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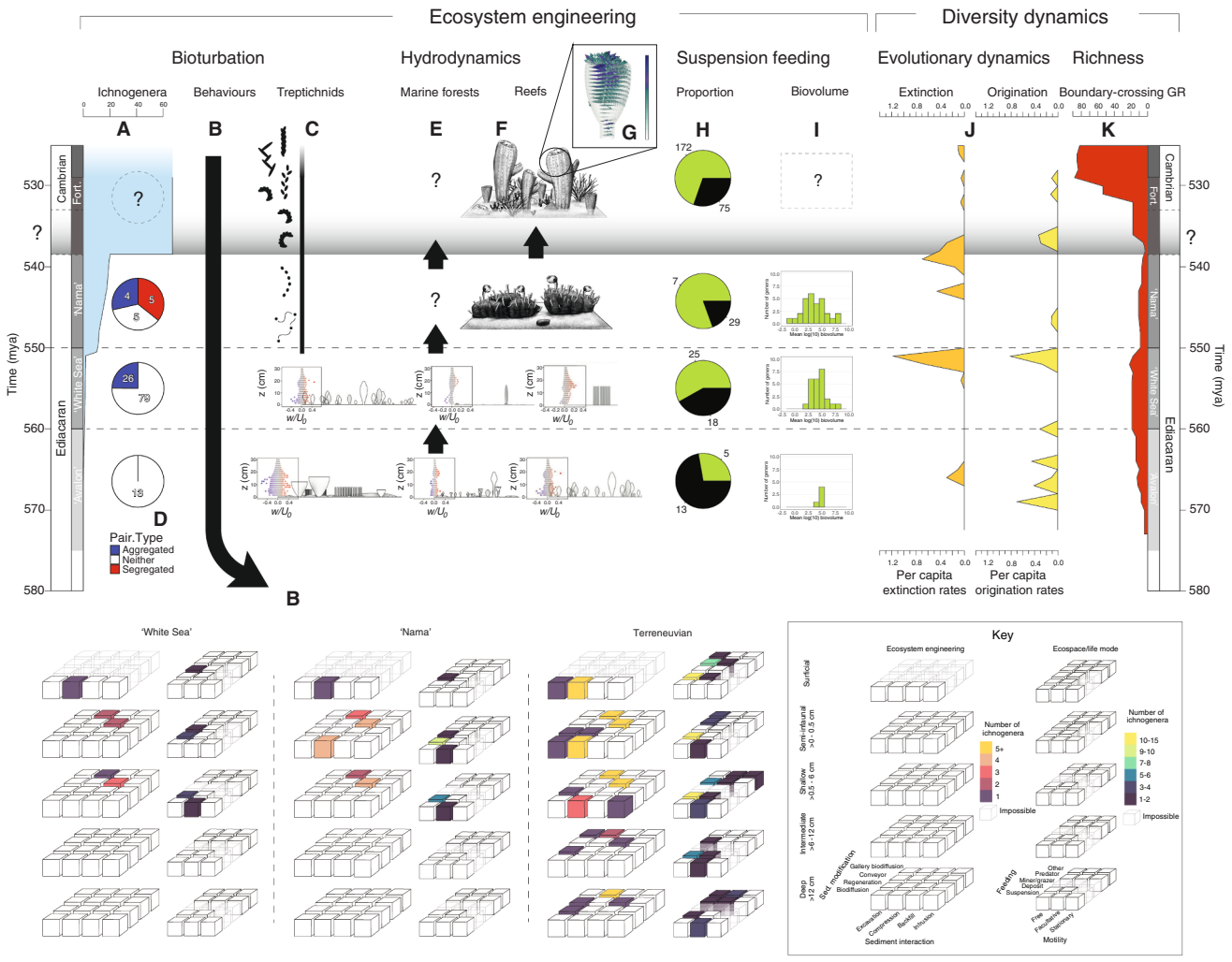
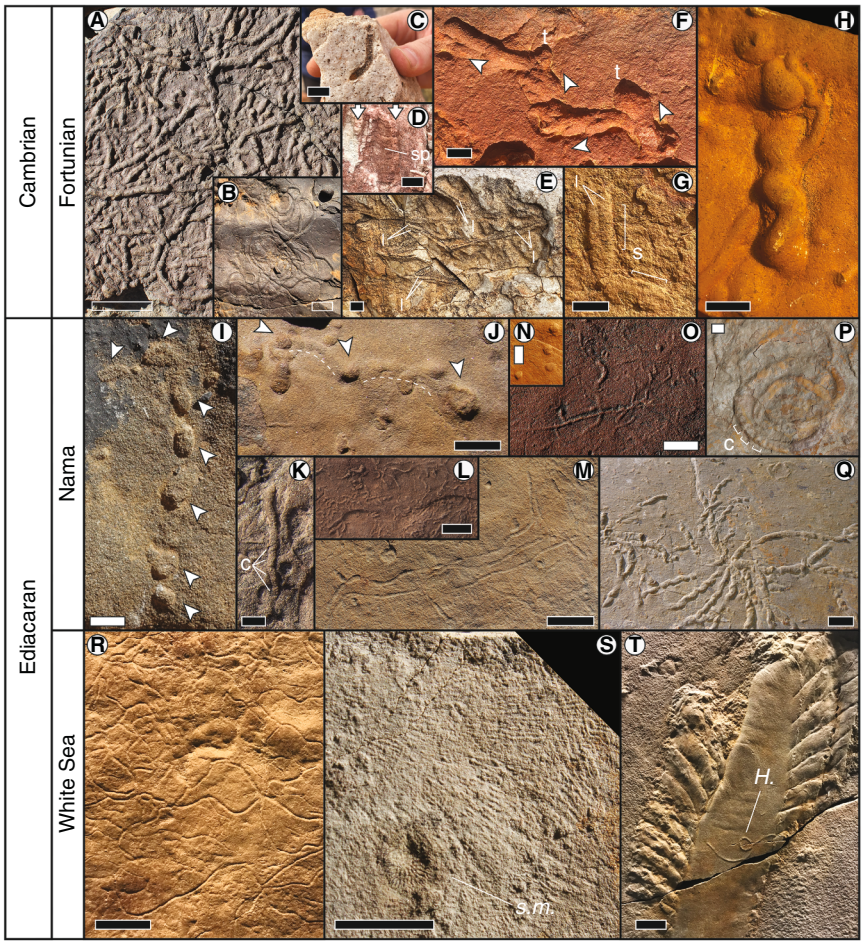


Figure 2. The rise of animal ecosystem engineering across the Ediacaran–Cambrian transition.
Current knowledge, and emerging approaches to both recognizing and quantifying the rise of metazoan ecosystem engineering across the Ediacaran–Cambrian transition, alongside a compilation of diversity dynamics including raw generic richness, origination rates and extinction rates (note the discrepancy in currently accepted ages for the Ediacaran–Cambrian boundary[48,49]). (A) Ichnogenus gamma diversity for the Ediacaran taken from our own compilation (Tables S2 and S3), and for the lower Cambrian from[61]. (B) Engineering and inferred feeding modes for Ediacaran and Cambrian tracemakers, plotted in multidimensional 'ecosystem engineering cubes' using methods developed by[122]; Ediacaran data from our own compilation, and Terreneuvian from[61]. (C) The stratigraphic range of treptichnid trace fossils across the Ediacaran–Cambrian transition; symbols reflect the evolving diversity of behaviours. (D) The effects of bioturbation on genus co-occurrence patterns; numbers give the proportion of non-random genus pairs within each assemblage that are structured (either aggregated or segregated) by bioturbation. The data indicate a growing proportion of segregation driven by bioturbation (modified from[14]). (E) Community hydrodynamics: plots of vertical velocity created by Avalon- and White Sea-aged communities, illustrating an increase in the disparity of mixing regimes associated with benthic marine forests (adapted from [119,120] (CC BY 4.0)). (F) Reef reconstructions from[94,97] for Ediacaran and Cambrian, respectively, illustrating an increase in topographic complexity. (G) Modelled fluid flow patterns through an archaeocyath sponge (*Archaeolynthus porosus*); recent work[102] suggests that these organisms were likely active suspension feeders and thus would have produced exhalent flows, substantially increasing fluid mixing above reef settings. (H,I) Plots showing the increasing proportion and individual biovolume of inferred suspension feeders across the Ediacaran–Cambrian transition. (J,K) Diversity dynamics shown in one-million-year bins and calculated from a new compilation of Ediacaran genus occurrences (Table S2), with refined dating of formations and individual localities provided by an extrinsic database using radiometric dates, isotopic excursions and superposition[137]. Origination and extinction rates are instantaneous, reflecting the negative log of the reciprocal of the proportion of genera known (or which disappear) after a one-million-year bin that first occur in that bin[138]. Genus richness is calculated as minimum standing richness given boundary-crossers (after[138]), i.e., genera with definite occurrences before and after that one-million-year interval.

question cuts to the heart of pervasive and long-running ideas in evolutionary biology. For example, the increasing intensity, diversity, and depth of bioturbation is thought to have been a central driver of the 'agronomic revolution'[71], with bioturbators oxygenating the subsurface, liberating nutrients and creating new habitats that Cambrian taxa could evolve in and exploit[72,73]. This specific tenet has recently begun to be tested with geochemical models[73]; the results suggest that late Ediacaran styles of bioturbation — at least initially — would have actually decreased oxygen in the shallow subsurface, and thus rather reduced habitat (although this effect is reversed with the greater depths and intensities of burrowing that emerge later in the



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Figure 3. Representative trace fossil taxa across the Ediacaran–Cambrian transition. These fossils illustrate the increase in bioturbative intensity, depth, behavioural complexity, and ecosystem engineering impact. (A) Dense assemblage of *T. pedum* (Swartkloofberg Formation; bed underside). (B) *Psammichnites* preserved on bed top (Uratanna Formation). (C) Unidentified J-shaped burrow, shown in cross section (Uratanna Formation). (D) U-shaped *Diplocraterion*, with vertical burrow limbs arrowed, and spreite ('sp') visible in the center (Parachilna Formation). (E) Assemblage of bilobed sediment-bulldozing traces resembling *Didymaulichnus* (Uratanna Formation; bed underside). (F) Large *Treptichnus* cf. *rectangularis*, illustrating characteristic 'probes' (arrowed) that terminate in bulbous lobes ('l'). (G) Bilobed ('l') trace resembling *Cruziana*, organized into distinct segments ('s'), and possessing faint scratch marks. (H) Horizontal, subsurface helical burrow resembling *Helicodromites* (Lintiss Vale Beds; bed underside). (I,J) Unnamed treptichnids (Urusis Formation; bed underside) preserving characteristic probes (arrowed) and linking burrows (dashed lines), illustrating the initial rise of bioirrigative behaviours. Treptichnids are now known from the White Sea–Nama transition ~551 Ma[80]. (K) *Torrowangea*, showing semi-regular constructions ('c') along its length. (L) Nest of meandering trace fossils resembling *Gordia* (Urusis Formation; bed underside). (M) *Helminthopsis* illustrating rudimentary avoidance behaviour (Urusis Formation; bed underside). (N) *Bergaueria* — simple, plug-shaped burrows (Urusis Formation; bed top). (O) Meiofaunal *Ariichnus* burrows (Urusis Formation; bed underside). (P) *Parapsammichnites* — potentially the oldest example of sediment bulldozing behaviour[78] (Urusis Formation). (Q) *Streptichnus*, illustrating characteristic cockscrew burrows and radiating burrow pattern (NESM-F-626; Urusis Formation). (R) Dense assemblage of *Helminthoidichnites* (SAM 42142; Rawnsley Quartzite). (S) Individual *Solza margarita* ('*S.m.*') on a surface dominated by *Kimberichnus* scratch marks (4853/186; Palaeontological Institute, Moscow, Russia). (T) Single *Helminthoidichnites*, preserved under an *Arborea* frond (SAM P49393; South Australia Museum, Rawnsley Quartzite). (Images (B) and (N) slab top surface; all others slab underside. White scale bars = 0.5 cm, black scale bars = 1 cm, open scale bars = 5 cm. All images: Simon Darroch.)

Cambrian). Consequently, Ediacaran burrowing is unlikely to have driven evolutionary radiation across the Ediacaran–Cambrian transition. If nothing else, however, this study demonstrates that combining fossil data with modelling approaches represents a powerful means for hypothesis testing.

Linking the emergence of bioturbation to extinction across the Ediacaran–Cambrian transition is more controversial, given the contemporaneous evidence for abiotic pulses of environmental stress[41,52,74]. However, debate on this topic has intensified with the recognition of two potential extinction pulses, one at the White Sea–Nama transition and another at the Ediacaran–Cambrian boundary itself[12,41,57,75] (Figure 2J). The first of these pulses is thought to have removed the majority of soft-bodied macrofossil clades that characterize the White Sea assemblage, while the second removed the remaining soft-bodied genera, along with many of the early biomineralizing forms[12,41]. Bioturbation has been hypothesized to have driven biotic turnover via several mechanisms: the mobilization of reactive organic matter, the destruction of microbial mats that organisms relied on and the re-suspension of sediment[59]. This latter process can interfere with both feeding and larval settlement of other benthic groups, such as filter-feeders — a process known as 'trophic group amensalism'[76]. In parallel, the growing diversity of Ediacaran trace fossil behaviours now includes a variety of ecosystem engineering impacts, including the first sediment bulldozing, active back-filling and gallery biodiffusive-type burrows[61,77–79] (Figure 2B). The majority of these traces represent an increase in biomixing[59], although shallow-tier gallery biodiffusers, represented here by treptichnids (Figure 3I,J), are key, representing the first major bioirrigative behaviours to appear in the late Ediacaran. Treptichnids are subsurface burrows characterized by semi-regular 'probes' that reach up towards the sediment–water interface, thus impacting both sediment rheology and the circulation of water through the subsurface. The recent discovery of sophisticated treptichnid behaviours shortly above an ash bed dated at ~550.1 Ma is particularly noteworthy[79]. Here, their appearance coincides with the last appearance of *Dickinsonia* — an iconic White Sea-aged taxon thought to be heavily reliant on microbial mats[80]. This discovery thus potentially closes the near seven million-year gap[14] separating a putative White Sea–Nama extinction pulse ~550 Ma and the first

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appearance of more complex and intense bioturbation behaviours (Figure 2C).

In addition to a broad coincidence in time between this first pulse of Ediacaran extinction and the first appearance of 'complex' bioturbation, there is both anecdotal and quantitative evidence to support some specific causative scenarios. For example, field-based studies have noted a change in the character, abundance, and distribution of microbial mats over the White Sea–Nama transition[59,81], perhaps suggesting that intensifying bioturbation was beginning to change the substrate. Several clades of soft-bodied macrofossils disappear over this same interval, many of which are thought to have relied on mats either as a substrate for attachment, or as a food source[82]. In addition, the morphology of inferred suspension feeders change substantially over the White Sea–Nama transition, with a switch from extreme low-relief (<1 cm) and mat-adapted discoidal taxa[83,84], to groups with a greater variety of body plans occupying higher tiers in the water column and new ecological niches[85–87] (Figure 2H,I). This pattern is what one might expect from a scenario involving trophic group amensalism[76]. Lastly, two recent co-occurrence analyses have revealed a substantial shift in community structure over the White Sea–Nama transition associated, at least in part, with the growing prevalence of bioturbated surfaces, along with increased evidence for niche separation[14,46] (Figure 2D). There are thus plausible cause-and-effect scenarios linking bioturbation with forms of ecological stress, and which may have helped to drive biotic turnover.

Suspension feeding

Suspension feeding — a feeding mode by which sessile animals remove food particles from the water column — plays vital engineering roles in reducing turbidity and increasing the depth of light penetration[88]. Suspension feeding also drives more efficient transport and burial of organic carbon, contributes more to the deposition of fine sediment in shallow water environments, and forms energetic links between the benthic and pelagic realms[89,90]. These processes are particularly well-studied for dense assemblages of filter feeders, such as mussels[88], where they combine to stimulate the growth of submerged aquatic vegetation.

The first macroscopic suspension feeders are thought to have emerged as part of the Avalon-aged Mistaken Point communities[91], diversified in the White Sea assemblage[83] and are represented among the earliest biomineralizing metazoans in the Nama assemblage where they colonise stromatolitic reef-tops. Although reconstructing the feeding mode of many Ediacaran taxa is difficult, recent work using computational fluid dynamics modelling has also helped to identify likely suspension feeders among some of the enigmatic, soft-bodied groups[83–86], thus providing the foundation for quantifying changing abundance and diversity during the Ediacaran–Cambrian transition.

A late Ediacaran rise in suspension feeding is thought to have played an important role in structuring communities during this period. Our compilation of inferred feeding modes (Table S3) suggests both a growing prevalence of these suspension feeders through the late Ediacaran, and that suspension feeders diversify in body size (Figure 2I). This suggests a radiation into new niches, and potentially the exploitation of new food sources. Intuitively, the growing prevalence of suspension feeders would have led to enhanced carbon flux to seafloor sediments[92], which may have helped to fuel early phases of the Cambrian diversification of animals[86,93]. Testing this hypothesis is complex, as there are many unknowns. For example, the crux of the role played by suspension feeders in pelagic–benthic coupling in today's oceans lies in the production of mucus-bound faeces and pseudofaeces that sink to the bottom; however, almost nothing is known about the digestive anatomy or digestive processes of Ediacaran taxa. In addition, the engineering impacts of suspension feeding are likely dependent both on community density and the efficiency with which food particles are captured. Despite these difficulties, computational fluid dynamics offers a means for quantifying feeding efficiency in individual organisms[83], and in the future could be combined with numerical models to tackle this question.

Reef building

Reefs are critical components of modern marine ecosystems, responsible for a variety of ecosystem engineering processes that support biodiversity[94]. Reefs are characterized by structural complexity, and thus many of these processes arise from their interaction with the fluid environment, including controls on the intensity of seawater mixing, the creation of hydrodynamic refugia and the baffling of currents[95,96]. In turn, these impacts influence the vertical transport of heat, food, pollutants, pathogens, larvae, suspended loads and nutrients[96].

The Ediacaran–Cambrian transition marks two revolutions in reef building: first, the initial emergence of biomineralizing animals on stromatolitic reef tops in the late Ediacaran[92,97]; and second, the rise of the first genuine metazoan reef frame builders — calcifying sponges called archaeocyaths — in the lower Cambrian[94,98] (Figure 2F). These two revolutions led to increases in three-dimensional complexity, higher relief above the seafloor and higher surface roughness, likely to result in more turbulent flow over the tops of reef communities. Moreover, the emergence of metazoan reefs may have helped to drive diversification over the Ediacaran–Cambrian transition. As yet, the hydrodynamic characteristics of Ediacaran reefs have not been examined in the same way that communities of soft-bodied taxa have[85]. However, the impacts of Cambrian reefs on habitat creation have begun to be quantified. For example, although archaeocyath reef communities were not necessarily globally dominant[99], they were associated with higher species richness and higher diversity than settings without reefs — an effect that has apparently persisted throughout the Phanerozoic[100,101]. In addition, archaeocyaths were almost certainly actively 'pumping' fluid through pores during feeding[102] (Figure 2G), which would have been likely to result in substantial exhalent flows, enhancing mixing above communities and creating new ecological and evolutionary opportunity.

Biomineralization

The emergence of reefs is closely linked to the evolution of animal biomineralization, which is associated with other, unique engineering processes[103]. Calcareous shells expand the area of hard substrates available for attachment by other animals, and can also provide habitat for endolithic organisms. The physical structure of shells often creates interior refuges from predation or wave and current energy, whereas denser accumulations of shells can enhance habitat heterogeneity for organisms that dwell within the shell bed[104]. These effects can persist long after the death of the organism, altering flow in the seafloor boundary

layer, influencing sediment movement[105–107] and the transport of solutes and other particles[108].

Although organisms have occupied hard substrates throughout much of the history of life, the origination of macroscopic shells in the Ediacaran — principally the enigmatic taxa *Cloudina* and *Namacalathus* — marked the beginning of the transition to benthic ecosystems with hard substrates being increasingly engineered by animal shell production[109]. As with other processes discussed here, the scale and intensity of these engineering processes were lower than in the later Phanerozoic or modern times; Ediacaran shells apparently did not host epibionts (species adapted to using shells as an attachment substrate, the first evidence of which is known from the Cambrian[110,111]) but do preserve borings of endolithic cyanobacteria[112]. Moreover, Cambrian biomineralized organisms were comparatively small[113] and rates of shell production were also low, as indicated by thin shell beds[114] and a relatively small percentage of shelly material in limestones[115]. Nevertheless, the rapid expansion of biomineralization across multiple Ediacaran–Cambrian animal groups marks the start of a gradual transformation of the seafloor, into one where shells played an increasingly important role in ecosystem engineering.

Marine forests

Like reefs, 'marine forests' are communities of organisms living on the seafloor that perform a variety of vital engineering roles through their hydrodynamic interactions with currents. In the present day, marine forests are formed by seagrass, red-, green and brown algae, as well as epibenthic and endobenthic invertebrates. Together, these create complex, three-dimensional habitats that support diverse communities through current baffling, mixing of the water column and the concentration of food particles[116]. The first candidate communities with such functions appear in the Avalon interval, preserved in the famous fossil surfaces at Mistaken Point with communities of (largely) frondose organisms in deep water forming canopies of varying heights, and with specific spatial relationships on the seabed governed by reproductive mode[117].

Recent work has linked these engineering processes to macroevolutionary patterns over the Ediacaran–Cambrian transition. The first major jump in Ediacaran global diversity comes at the Avalon–White Sea transition ~550 Ma, with the migration of macrofauna into shallow water environments higher up on the continental shelf. Many of the explanations for this migration have focused on pulsed increases in global oxygen levels[118]; however, Ediacaran organisms themselves may also have helped to engineer environments conducive to the emergence of new body plans and more complex behaviours. Fluid dynamics modeling has shown that communities of frondose organisms preserved at Mistaken Point would have generated substantial vertical mixing in the water column, enhancing the transport of dissolved oxygen and dissolved organic carbon in the canopy[119]. In this fashion, these organisms are likely to have ventilated the Ediacaran seafloor on local scales, and thus potentially fostered the evolution of more energy-intensive life modes. Similar studies on the White Sea assemblage have shown that the transition to shallow water environments brought with it communities characterized by greater hydrodynamic variability[120] (Figure 2E). This was likely a substantial source of environmental heterogeneity that may have created ecological opportunity and fostered subsequent diversification.

Engineering 'regime shifts' and analogous intervals in Earth history

The brief review above illustrates that a wide variety of powerful new ecosystem engineering processes evolved during the Ediacaran–Cambrian transition, and that there are good reasons to suspect that these helped to drive pulses of both origination and extinction, via habitat creation, modification and substantial alteration of nutrient flows. We acknowledge, however, that many of these processes have only just begun to be recognized[121] and quantified[73,122], and thus specific cause-and-effect scenarios are hard to test. Taking the example of 'complex' bioturbation and a first pulse of Ediacaran extinction ~550 Ma[52,79], treptichnid trace fossils — though unquestionably present in the Ediacaran — were apparent opportunists, and thus locally abundant but regionally rare[59]. This raises the question whether and how local-scale engineering processes are able to produce global and long-term macroecological and evolutionary change. This is a central issue in paleobiology that has historically been hard to tackle[15,123], but recent conceptual advances link biotic engineering to fitness landscapes[124] and there are case studies linking (for example) the engineering impacts of reef ecosystems with diversification in both teleost fish[125] and benthic molluscs[126]. These examples from the younger Phanerozoic allow us to hypothesize a scenario where pulses of origination and extinction across the Ediacaran–Cambrian transition were driven by the emergence of new ecosystem engineering processes (Figure 4). Co-opting the recent idea[52] that the diversity drop over the White Sea–Nama transition reflects the replacement of stem-group taxa with crown-group clades, and with extinction driven by the engineering processes associated with more modern animal groups, we can begin to articulate specific cause-and-effect scenarios. New simulations-based approaches[16] represent a means by which these hypotheses may be tested in the future, and an exciting frontier in paleobiology.

More broadly, this lends support to the notion of a distinct ecosystem engineering regime shift over the Ediacaran–Cambrian transition. The term 'regime shift' has been used to describe ecosystems switching between alternative stable states[127]; however, here we use it in the context of a geologically (relatively) rapid change in the biotic processes governing resource flows on both global and local spatial scales. On short timescales newly appearing ecosystem engineering processes almost certainly resulted in changes in nutrient flows, patterns of habitat disturbance and the topography and rheology of the substrate. On longer timescales, we hypothesize that these gave rise to new rules of community assembly, new ecological niches, and altered macroevolutionary trajectories. In this light, the Ediacaran–Cambrian transition marks a major inflection point in Earth history, driven by the emergence of ecosystem engineering processes that continue to exert powerful controls on the structure of communities in the present day[57]. This notion of an engineering regime shift dovetails with two other perspectives; first, linking the emergence of metazoan ecosystem engineering to permanent alterations to the fitness landscape[47], in turn driving the emergence of new feeding modes and step-wise construction of the 'Eltonian pyramid' (i.e., a more modern structure

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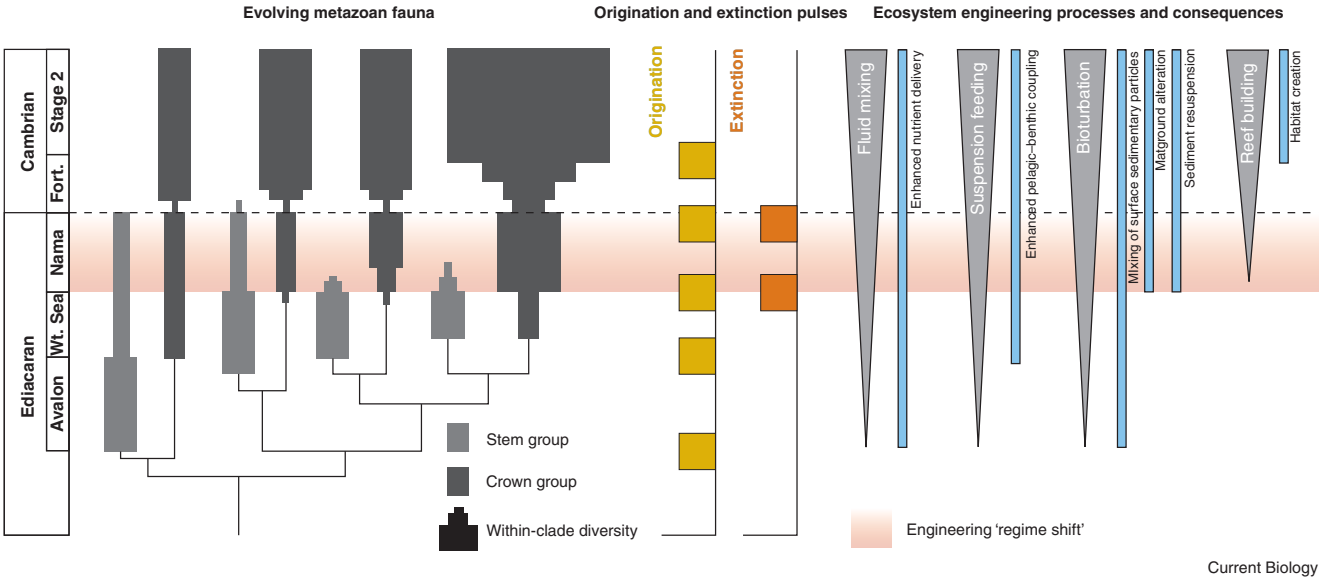


Figure 4. Hypothetical model for the emergence of novel ecosystem engineering processes as drivers of macroevolutionary dynamics. Based on the emerging datasets shown in Figure 3. Spindle diagram on left modified from recent models[52]. Ecosystem engineering impacts split into processes and consequences, following[1,5]. In this hypothesis, pulses of origination and extinction are driven by the appearance of new metazoan ecosystem engineering impacts, with an interval of biotic turnover at the White Sea–Nama transition, corresponding to engineering impacts associated with more modern, crown-group animal clades. The White Sea–Nama transition would thus mark a crucial inflection point separating two, markedly different engineering 'regimes'. We note that this figure is strictly theoretical, and is designed to help structure hypotheses that can be tested using the techniques outlined elsewhere in this review. Moreover, this model does not exclude the possibility of turnover driven by environmental perturbation and other sources of ecological stress, such as those recently proposed for the Ediacaran–Cambrian boundary[139] (adapted from[52] (CC BY 4.0)).

of trophic webs, including secondary and tertiary consumers). Second, this is close to the notion of a 'Phanerozoic Earth system'[4], although re-framed in the context of an inflection point between a Precambrian world dominated by Earth-system engineering processes and a world with ever-increasing numbers of ecosystem engineering processes. We argue that the crucial step in this regime shift occurred over the White Sea–Nama transition, and that the long-term ecological and evolutionary consequences of this change are starting to be detected[14,46].

In turn, these inferences offer a potential answer to the first of our two questions ('has the emergence of new biotic engineering processes been distributed evenly throughout time, or rather clustered during specific intervals?'). Given that so many ecosystem engineering processes are unique to animals[4,57], the Ediacaran–Cambrian transition undoubtedly represents a substantial increase in planetary bioengineering and a significant step towards the structure and function of the modern marine biosphere. A full answer would require a comprehensive account of engineering-type processes throughout Earth history. Regardless, the Ediacaran–Cambrian transition stands out as a crucial supporting datapoint. The second question ('has the emergence of new engineering driven intervals of evolutionary radiation, or extinction?') is more complex; the answer is almost certainly 'yes', but establishing cause-and-effect requires that engineering processes associated with long-extinct organisms be quantified. The tools necessary for this are realistically only now being developed[10,61,73], but pursuing these questions is worthwhile, as they offer a window into understanding the biotic factors that have helped shape the trajectory of life, including pulses of origination and — potentially — extinction.

On this last point, potential Phanerozoic analogues to pulses of extinction over the Ediacaran–Cambrian transition have been proposed. Combining fossil and geochemical data have produced support for linking pulses of Devonian extinction to the expansion of green plants on land, via deeper rooting systems, the release of terrestrial phosphorous, and marine anoxia[128,129]. Similar biotic drivers have been proposed for the first pulse of end-Ordovician extinction, with the expansion of non-vascular and early vascular land plants accelerating chemical weathering, thereby triggering the growth of ice sheets and the shrinking of shallow marine habitats[130,131]. Emerging from this growing body of literature, therefore, is support for the idea that evolution, and the emergence of new engineering behaviours, may have ultimately driven major biotic turnover events in Earth history.

Perhaps the most ambitious comparison, however, is with anthropogenic engineering processes driving the present-day biodiversity crisis[52]. Human ecosystem and Earth system engineering includes the alteration and fragmentation of physical habitats, the construction of specialized microhabitats and the harnessing of new energy sources[132,133] — all, arguably, similar to the consequences of the rise of animals over the Ediacaran–Cambrian transition. In turn, these have contributed to increased extinction rates[134], have re-shaped community assembly processes[135] and are re-shaping long-term evolutionary opportunity[136]. In this light, the emergence of humans may represent the latest regime shift in biotic engineering, and potentially the only one currently understood to be driven by a single species. Establishing whether the Ediacaran–Cambrian transition represents a reasonable (or useful) analogue for the Anthropocene[52]

will require targeted work. However, the possibility is fascinating and may offer a new way to understand major transitions in the history of life.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

Supplemental information including two figures, three tables and methods can be found with this article online at https://doi.org/10.1016/j.cub.2026.08.056.

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