

How to engineer a habitable planet: the rise of marine ecosystem engineers through the Phanerozoic

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Abstract: Ecosystem engineers are organisms that modify their physical habitats in a way that alters resource availability and the structure of the communities they live in. The evolution of ecosystem engineers over the course of Earth history has thus been suggested to have been a driver of macroevolutionary and macroecological changes that are observed in the fossil record. However, the rise to dominance of ecosystem engineers has not been thoroughly reconstructed. Here, we investigate the history of bioturbation and reef-building (two of the most important marine ecosystem engineering behaviours today) over the Phanerozoic. Using fossil occurrences from the Paleobiology Database, we reconstruct how common communities influenced by ecosystem engineers were in the oceans, how dominant ecosystem engineers were within their own communities, and the taxonomic and ecological composition of

bioturbators and reef-builders. We find that bioturbation has become an increasingly common ecosystem engineering behaviour over the Phanerozoic, while reef-building ecosystem engineers have not become more dominant since their Devonian apex. We also identify unique bioturbation and reef-building regimes that are characterized by different ecosystem engineering taxonomic groups, ecological modes, and dominance, suggesting that the nature of ecosystem engineering has at times rapidly shifted over the course of the Phanerozoic. These reconstructions will serve as important data for understanding how ecosystem engineers have driven changes in biodiversity and ecosystem structure over the course of Earth history.

Key words: ecosystem engineering, bioturbation, reefs, Phanerozoic.

THE present-day structure and function of Earth's global ecosystems are the result of the continuous co-evolution of life and Earth systems processes that has occurred over billions of years. The Earth's physical systems (i.e. the hydrosphere, lithosphere, atmosphere and cryosphere) and its biosphere interact as synergistic components of a larger, ever-evolving complex system; a concept most famously invoked by the Gaia Hypothesis (Lovelock 1972; Lovelock & Margulis 1974). In this framework, Lovelock (1995) defined the co-evolution of life and the Earth: 'Biota influence their abiotic environment, and that environment in turn influences the biota by Darwinian process.' The latter half of Lovelock's definition of co-evolution has been thoroughly investigated by palaeobiologists, particularly in the abundant research linking together the fossil, sedimentological, and geochemical records to understand how environmental change in the past impacted macroevolutionary processes. Well-documented examples include environmental drivers of macroevolution such as dynamic ocean redox conditions (Wood & Erwin 2018), ocean chemistry (Stanley 2006), the character and volume of marine

sedimentation (Heim & Peters 2011), and tectonics (Davis 2005; Smiley *et al.* 2024). Meanwhile, the first part of this definition (that organisms can drive macroevolutionary dynamics by influencing their abiotic environments) has perhaps historically been overlooked by palaeobiologists as a driver of evolutionary dynamics.

Ecosystem engineering broadly refers to the processes by which organisms interact with their physical environments in a way that modifies resource flows and thereby impacts the structure and function of communities (originally defined by Jones *et al.* 1994; see e.g. Reichman & Seabloom 2002, Hastings *et al.* 2007, Berke 2010, for discussion of longstanding debates on nuances of these definitions). Ecosystem engineers are a diverse ecological functional group, encompassing dam-building beavers, vegetation-trampling herbivores, sediment-mixing invertebrates, and reef-building corals (e.g. Jones *et al.* 1994; Meysman *et al.* 2006; Trepel *et al.* 2024). Despite being a well-accepted concept in ecology, with established diverse effects on ecological dynamics on a variety of temporal and spatial scales (Romero *et al.* 2015; Guy-Haim *et al.* 2018; Albertson *et al.* 2024), ecosystem engineering

is not particularly well-studied in the fossil record as a type of biotic interaction that can drive ecological change on longer, evolutionary timescales. Establishing the role that ecosystem engineers play in driving ecological and evolutionary dynamics is a key component of understanding how biotic interactions have shaped biodiversity over the Phanerozoic. It has long been proposed, for example, that the rise of ecosystem engineers triggered increases in biodiversity over the course of the history of animal life (Erwin 2008). However, it has not yet been quantified when and how the ocean's major ecosystem engineers, which hold critical ecological importance in their communities, came to their dominance.

Here, we investigate the rise of two of the most important marine ecosystem engineering behaviours recognized in the modern oceans: bioturbation and reef-building (Jones *et al.* 1994). In quantifying the importance of these groups in a deep-time context, we ask two broad questions: (1) How prevalent have these two ecosystem engineering groups been throughout earth history? and (2) How might have ecosystem engineering processes changed as evolution occurred within these broad groups? Using fossil occurrences from the Paleobiology Database (PBDB; <https://paleobiodb.org/>) (Alroy 2008), we reconstruct three ecosystem engineering trends through the Phanerozoic: quantifying how pervasive ecosystem engineers have been in a range of different environments, how dominant ecosystem engineers have been within their own communities, and identifying how engineering taxa have been partitioned among various ecological roles and taxonomic groups. These data help us better understand the rise and fall of animal ecosystem engineering behaviours over the last c. 540 million years, and will facilitate future work quantifying how these ecosystem engineers may have driven global-scale evolutionary and ecological changes throughout the Phanerozoic.

Ecosystem engineering in the fossil record

In modern systems, ecosystem engineering processes are often divided into two distinct frameworks: outcome-based, or process-based (Berke 2010). Process-based ecosystem engineering frameworks are concerned with the behaviours of ecosystem engineers and the environmental changes they cause, while outcome-based ecosystem engineering frameworks are concerned with the evolutionary and ecological changes that arise as a result of the environmental change (Berke 2010). Ecologists tend to focus on ecosystem engineering processes (perhaps because the burden of ecological significance is difficult to establish on short time scales; Berke 2010) and palaeoecologists have traditionally followed suit in attempting to constrain the environmental effects that ancient ecosystem engineers

have imparted on their habitats, often by using a combination of sedimentological, geochemical, and modelling approaches (Morris *et al.* 2015; Herringshaw *et al.* 2017; Dhungana & Mitchell 2021; Cribb *et al.* 2023; Manzuk *et al.* 2023).

However, we argue that the fossil record is potentially more appropriate for understanding ecosystem engineering outcomes, and moreover can shed light on how (on long timescales) the emergence of new ecosystem engineering behaviours can scale up to create whole new habitats, ecospace, and niches (Erwin 2008), thus changing adaptive landscapes and creating new evolutionary opportunities. Recognizing the crucial role these feedbacks may have played early in the evolutionary history of eukaryotes, Butterfield (2011) coined the term 'evolutionary engineers' to describe this phenomenon. Usefully, many of the long-term ecological changes associated with common ecosystem engineering behaviours are readily preserved in the rock record. However, it is difficult to robustly connect ecological changes driven by ecosystem engineering to animals like bioturbators and reef-builders themselves unless we have a robust history of changes in their abundance, dominance, and ecology. Therefore, by first studying the rise of ecosystem engineers throughout Earth history, we can later begin to understand how their activities have influenced macroecological and macroevolutionary dynamics and begin to address the role that ecosystem engineers have played in shaping present-day patterns in biodiversity.

Bioturbation

Bioturbation refers to the sediment mixing done by organisms living on and within sediments; in this case, the ocean seafloor. Bioturbators have long been recognized as major marine ecosystem engineers for their effects on sediment biogeochemistry, seafloor rheology, and resource availability in benthic ecosystems (Jones *et al.* 1994; Meysman *et al.* 2006). Bioturbation can be further divided into two end-member processes, based on how the organism interacts with the sediment: biomixing and bioirrigation. Biomixing refers to the reworking of solid-state particles (e.g. mineral grains, particulate organic matter, microorganisms) as the animal moves through the sedimentary matrix (Kristensen *et al.* 2012). Bioirrigation, on the other hand, refers to the enhanced transport of pore waters and solutes within the sediment itself and between the sediment and overlying water column (Kristensen *et al.* 2012). Although in practice the construction of any burrow results in both biomixing and bioirrigation, these two end-members are generally associated with specific feeding behaviours and ecological strategies. Deposit feeders and grazers tend to be more

effective biomixers, while suspension feeders tend to be more effective bioirrigators (Kristensen *et al.* 2012). Bio-mixing and bioirrigation have been demonstrated to have variable, and even opposite, impacts on the cycling of key nutrients in benthic ecosystems (van de Velde & Meysman 2016; van de Velde *et al.* 2020; Tarhan *et al.* 2021; Cribb *et al.* 2023). Therefore, ecosystem engineering impacts are not equal between all infauna, but are instead a function of the bioturbator's potential for mixing intensity, mode of locomotion, and feeding behaviour (Herringshaw *et al.* 2017).

Reef building

Reef-builders are among the most important ecosystem engineers in modern oceans, responsible for creating three-dimensional structures that support a wide diversity of other taxa, perform vital biogeochemical functions, and produce hydrodynamic patterns that create unique habitats and influence resource flows (Sebens *et al.* 1998; Monismith 2007; Wild *et al.* 2011; Davis *et al.* 2021). Today, Scleractinia are the dominant coral reef-builders in the ocean, but other taxonomic groups have occupied that role throughout Earth history. Organisms have been constructing reefs for billions of years, starting with the formation of stromatolite reef complexes in the early Archaean (Allwood *et al.* 2006). Metazoan reefs developed much later with the colonization of reef-top settings by the enigmatic and biomineralizing taxa *Cloudina* and *Namacalathus* in the Ediacaran (Penny *et al.* 2014). The taxonomic diversity of metazoan-reef builders increased dramatically throughout the Phanerozoic, with sponges, bivalves, brachiopods, bryozoans, gastropods, tube worms and corals constructing major Phanerozoic reefs at various intervals throughout Earth history (Wood 1993; Kiessling 2002, 2009).

Reef-builders generate habitat complexity, and greater reefal habitat complexity is positively associated with biodiversity, speciation, and ecosystem resilience (Kiessling *et al.* 2010; Wild *et al.* 2011; Cheung *et al.* 2021). Therefore, groups of reef-builders that contribute to greater habitat complexity are, in theory, more effective ecosystem engineers. True reef-builders, such as scleractinian corals which form rigid frameworks with significant relief above the seafloor, are presumably more effective ecosystem engineers than, for example, biostrome-builders, which form dense skeletal material on the seafloor with little to no topographic relief. However, a framework of ancient reef ecosystem engineering impact (similar to Herringshaw *et al.* 2017 for bioturbation impact based on trace fossils) which incorporates various classification models of reef structure is an important avenue for future research.

METHOD

Dataset assembly

Marine body fossil occurrences were downloaded from the PBDB. The data were downloaded on 1 November 2023, using the following parameters: time intervals = Cambrian through Holocene; environment = 'any marine'; additional output blocks = 'ecospace', 'stratigraphy', 'stratigraphy ext.', 'geological context', 'lithology', 'lithology ext.'. The dataset was filtered and cleaned to remove uncertain taxonomic assignments, ichnotaxa, and form taxa, as well as fossil occurrences that had no formation assignments or ambiguous formation assignments (i.e. formation names that are simple lithological descriptions spanning across time and space). We stratigraphically binned the cleaned dataset into stages using the R package *divDyn* (v0.8.2) following Kocsis *et al.* (2019) and removed any fossil occurrences for which a stage could not be assigned. The entire cleaned PBDB dataset consists of 565 014 fossil occurrences representing 27 501 genera. Fossil occurrences were classified as bioturbators and reef-builders based on the inferred propensity for the fossilized animal to do either ecosystem engineering behaviour (as opposed to, for example, occurrences of trace fossils to document the rise of bioturbation). We use bioturbation to broadly include both biomixers and bioirrigators, as both processes have important ecosystem engineering impacts (Meysman *et al.* 2006). The dataset of bioturbating ecosystem engineers was constructed by collating occurrences of all infaunal genera (identified based on 'life habit' information in the PBDB that references infaunal tiering) and sediment bulldozing genera (identified based on 'life habit' information in the PBDB that references epifaunal, actively mobile, grazers and deposit feeders). This collated dataset was then further manually cleaned to remove taxonomic groups which are known to not be solitary and/or not bioturbators. The resulting bioturbator dataset consists of 130 406 fossil occurrences representing 4173 unique genera over the Phanerozoic. To construct our reef-building dataset, we focus here specifically on metazoan reef-builders and ignore structures such as microbialite and algal reef structures. We broadly include reef-building taxa that construct the four reef types defined by Kiessling & Flügel (2002) (true reefs, reef mounds, mud mounds and biostromes) as all four types of reef will have some ecosystem engineering impact, from constructing three-dimensional structures with topographic relief above to seafloor to impacting the physical characteristics of the seafloor. Ultimately, we construct our reef-builder dataset to focus on 10 major reef-building metazoan groups that have been previously identified as major reef-builders throughout Earth history

(Kiessling & Flügel 2002): archaeocyathids, stromatoporoids, glass sponges (hexactinellids), rudist bivalves, hydrozoans, chaetetids, tube worms, tabulate corals, rugose corals, and scleractinian corals. This reef dataset comprises 54 722 fossil occurrences representing 2268 genera over the Phanerozoic. The majority (81%) of these fossil occurrences are corals.

Analysis

For both bioturbators and reef-builders, we reconstructed the dominance of environments impacted by ecosystem engineers through the Phanerozoic by calculating the proportion of formations that contain at least one ecosystem engineering bioturbator or reef-builder in each stage. We also reconstructed how dominant ecosystem engineers were within their own environments by calculating the average proportion of fossil occurrences that are ecosystem engineers across all formations for each stage. Finally, we reconstructed the relative abundance of bioturbation feeding modes and phyla and reef-building taxonomic groups in each stage, also identifying the main bioturbation feeding mode or reef-builder group in each stage to identify major changes in ecosystem engineering regimes. For bioturbators we focused on the dominant feeding behaviour because it is most closely linked with bioturbation mode (biomixing or bioirrigation) and ecosystem engineering impact (e.g. Kristensen 2000; Herringshaw *et al.* 2017; Minter *et al.* 2017). For reef-builders, we used the dominant group out of the 10 taxonomic groups listed previously (see Kiessling & Flügel 2002).

To account for unequal numbers of fossils in different geological stages, we applied a subsampling method using an occurrence-level bootstrap protocol. To determine the proportion of formations possessing ecosystem engineers, we iteratively (1000 times) subsampled $n = 750$ occurrences per stage for our entire PBDB dataset, divided the data into ecosystem engineering (reef-building or bioturbating) and non-ecosystem engineering, and calculated the proportion of formations that contain at least one ecosystem engineer out of all fossiliferous formations in that stage. To determine the dominance of ecosystem engineers within their own formations, we also iteratively (1000 times) subsampled $n = 750$ occurrences per stage, further subsampled each formation containing ecosystem engineers to 20 occurrences per formation to minimize biases arising from uneven collection efforts, calculated the proportion taxa in each formation that are ecosystem engineers, and then took the mean proportion across all of those formations in that stage. To determine the relative abundance of different taxonomic groups contributing to reef-building and bioturbation, we restricted the

entire dataset to just those containing either bioturbators or reef-builders, iteratively (1000 times) subsampled $n = 250$ occurrences from these datasets, and calculated the proportion of fossils belonging to each bioturbation feeding mode or phylum and reef-builder group in each stage. Our subsampling protocol thus broadly controls for unequal numbers of fossils through time, but does not account for unequal numbers of formations and or sampled rock volume through time; however, because we express results as proportions (e.g. the proportion of formations possessing ecosystem engineers), we do not believe this to be a substantial source of bias (see also Heim & Peters 2011). By performing our subsampling routines, we created a distribution of results that represents a sample-standardized estimate of the relative prevalence of ecosystem engineers through time. In our figures illustrating these data, we show the mean value of these distributions in each stage.

RESULTS

Phanerozoic trends in bioturbation

There is a general positive trend in how common formations that contain bioturbators are throughout the Phanerozoic (Fig. 1). The proportion of fossiliferous formations that preserve bioturbating taxa is initially very high in the Cambrian (for example, $41.9 \pm 5.19\%$ of Stage 2 fossiliferous formations preserve bioturbators), but then declines to low proportions throughout the remainder of the early Palaeozoic. At the beginning of the Carboniferous, this proportion begins steadily increasing for the remainder of the Phanerozoic. In other words, the prevalence of communities that are impacted by bioturbating ecosystem engineers has been steadily increasing throughout the Phanerozoic, particularly since the Carboniferous (Fig. 1). This positive trend since the Carboniferous broadly persists even with analyses that are constrained within equal palaeoenvironments (Fig. S1). This positive trend is slightly stronger in shallow siliciclastics, which have greater proportions of formations containing bioturbating taxa in the Mesozoic and Cenozoic. There are also more dynamic changes around this upward trajectory in the deep siliciclastic and carbonate facies, although the upward trend still broadly persists. Across all environments, there are notable decreases in the proportion of formations that contain bioturbators which punctuate this upwards trend, most notably at the Carboniferous–Permian boundary, between the Induan and Olenekian in the wake of the end-Permian mass extinction (EPME), at the Triassic–Jurassic boundary, at the end of the Jurassic during the Tithonian, and between the Aptian and Albian during the Cretaceous (Fig. 1).

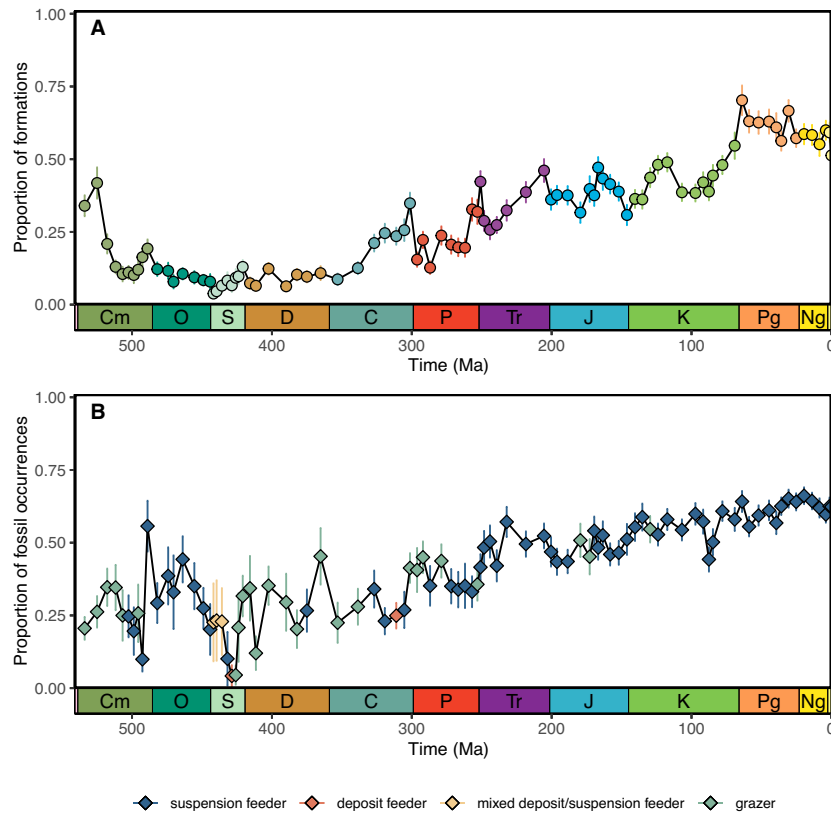


FIG. 1. Dominance of bioturbating ecosystem engineers over the Phanerozoic in terms of the number of formations globally (A) and within their own environments (B). A, proportion of formations that contain at least one bioturbating ecosystem engineer per stage; point colours correspond to periods on the x-axis. B, average proportion of taxa that are bioturbators across all formations containing bioturbating ecosystem engineers, with points coloured to represent the dominant feeding mode in that stage; point colours correspond to feeding mode in bottom legend. Data points are the average value of 1000 bootstrap subsampling iterations for each stage, and error bars are the 5th and 95th quantiles. Where error bars are not shown, point character size is larger than error. *Time scale abbreviations:* Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Palaeogene; Ng, Neogene. Note that Quaternary is too small to be labelled but represents the final two points on each panel. Geological timescale is visualized using the R package *deptime* (v1.1.1; Gearty 2023).

Similarly, there is a positive trend in how dominant bioturbating ecosystem engineers are within their own environments (Fig. 1). In the early Palaeozoic, the proportion of taxa that are bioturbators within their own formations increases through the early Cambrian, followed by a small decrease through the end of the Cambrian followed by a peak in dominance in Stage 10 ($55.6 \pm 7.94\%$ of occurrences), and then falls to an all-Phanerozoic low in the Silurian during the Homerian ($4.24 \pm 2.07\%$) (Fig. 1). From the Devonian onwards, bioturbators have become increasingly dominant within the formations in which they are preserved (Fig. 1). This upward trajectory of within-formation dominance persists even when analyses are constrained within individual palaeoenvironments, although the proportion of taxa that are bioturbators within these formations has been subtly declining during the Cenozoic for carbonate facies (Fig. S2).

Meanwhile, there are shifts in the ecological and taxonomic composition of bioturbating ecosystem engineers. Grazers were the most common group for most of the Cambrian (Figs 1, 2), primarily represented by molluscs (Fig. 3). For the rest of the early Palaeozoic, suspension feeders were dominant until the late Silurian (Fig. 1), with increases in the relative abundance of predators and deposit feeders (Fig. 2) concurrent with increases in the relative abundance of brachiopods, arthropods and annelids (Fig. 3). Grazing then became the dominant feeding behaviour through the remainder of the Silurian, the Devonian, and the early Carboniferous, after which the dominant feeding behaviour changed between suspension feeding, deposit feeding, and grazing up until the start of the Triassic (Figs 1, 2). During this time interval, molluscs were still the dominant bioturbators, but arthropods began to make up a significant portion of bioturbating ecosystem engineers as brachiopods had significantly

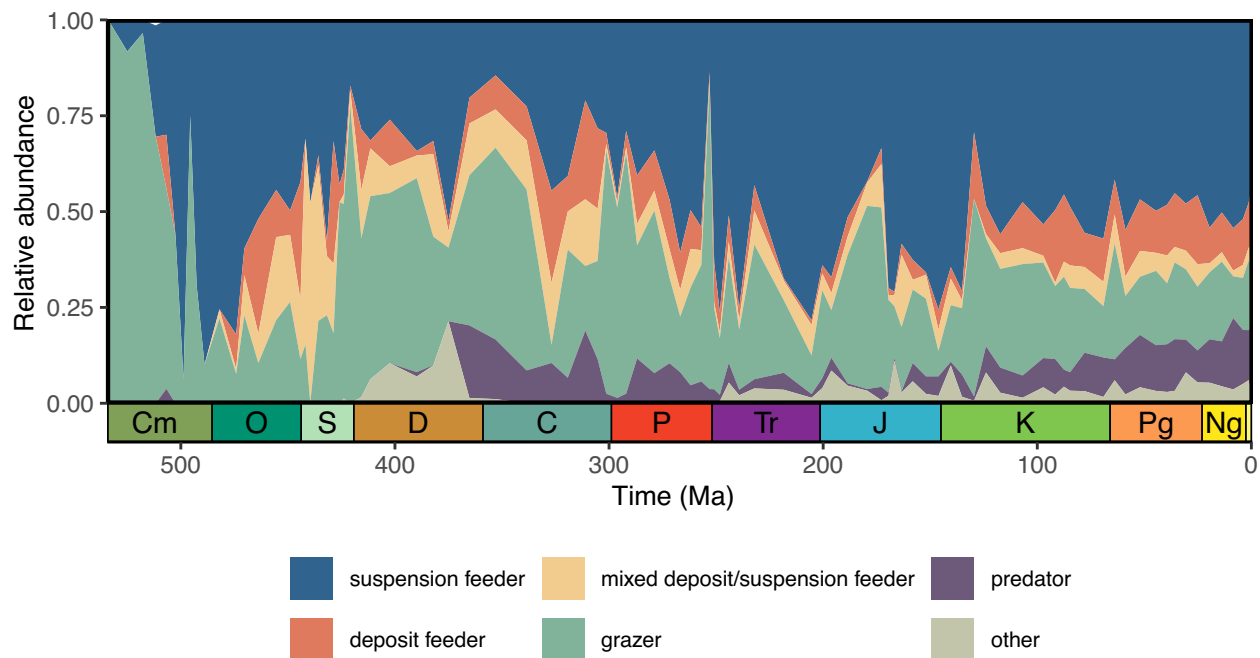


FIG. 2. Relative abundance of feeding modes of bioturbating ecosystem engineers over the Phanerozoic. Ribbon colours correspond to six feeding modes in the bottom legend. Data shown are the average of 1000 bootstrap subsampling iterations for each stage. See Figure 1 for timescale abbreviations. Geological timescale is visualized using the R package *deeptime* (v1.1.1) (Gearty 2023).

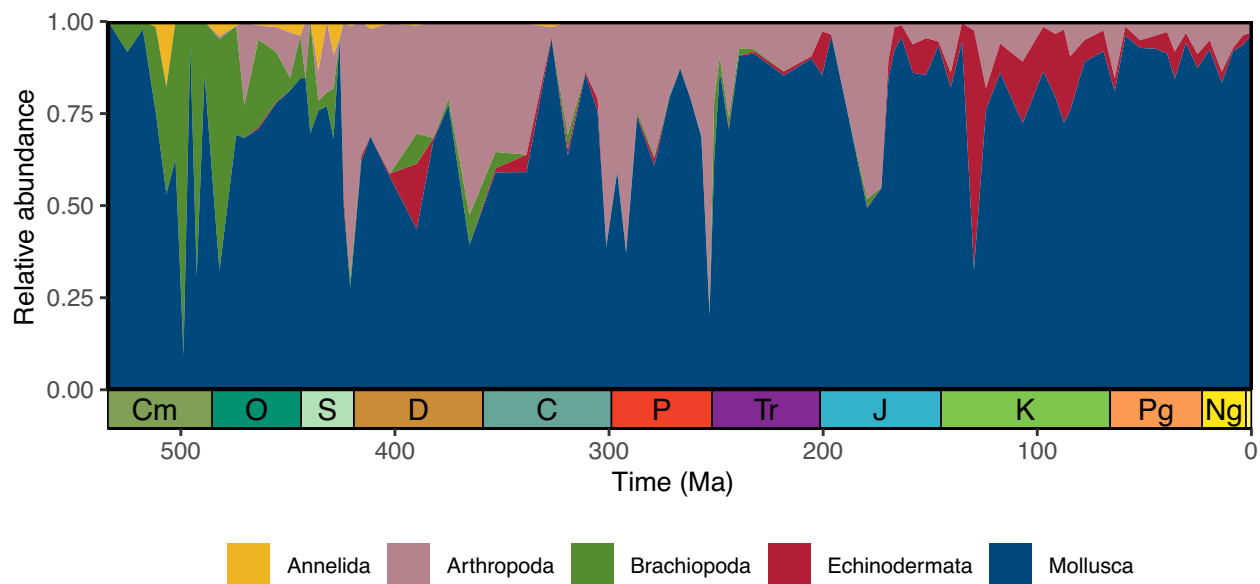


FIG. 3. Relative abundance of phyla of bioturbating ecosystem engineers over the Phanerozoic. Ribbon colours correspond to five phyla of bioturbators in the bottom legend. Data shown are the average of 1000 bootstrap subsampling iterations for each stage. See Figure 1 for timescale abbreviations. Geological timescale is visualized using the R package *deeptime* (v1.1.1) (Gearty 2023).

declined (Fig. 3). For the remainder of the Phanerozoic, suspension feeders represented the dominant feeding behaviour among bioturbators, other than for brief intervals in the Jurassic and Cretaceous when grazers regained dominance (Figs 1, 2). From the Triassic onwards,

molluscs were the dominant bioturbating phylum, with arthropods and echinoderms representing the majority of the remaining bioturbators (Fig. 3). During the intervals in the Jurassic and Cretaceous when grazing was the dominant feeding behaviour, arthropods and echinoderms

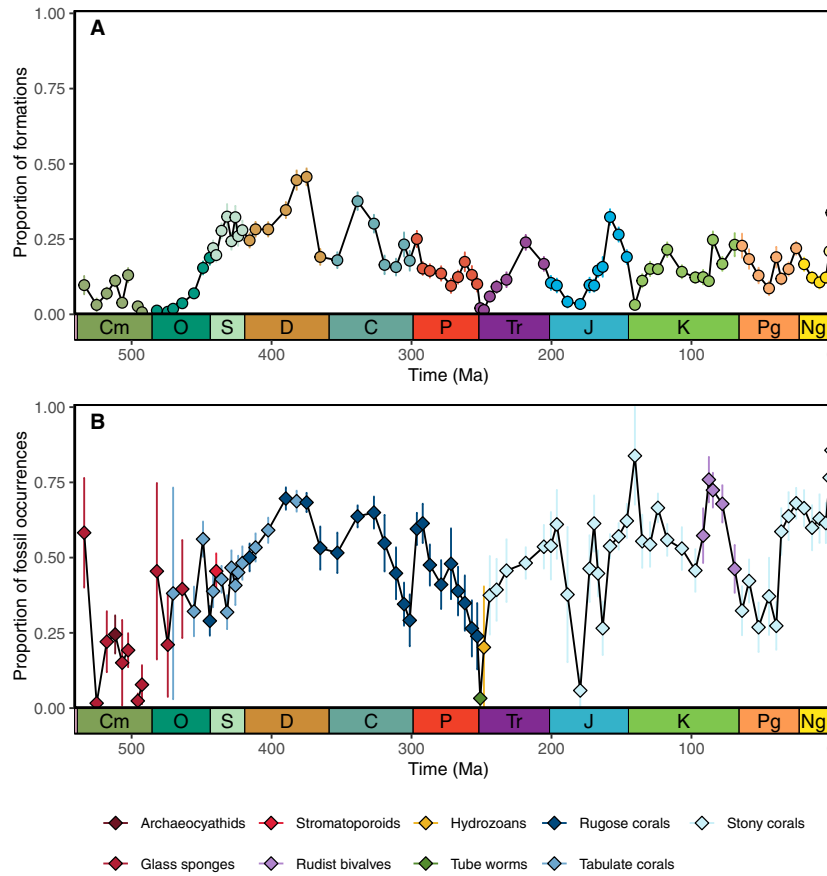


FIG. 4. Dominance of reef-building ecosystem engineers over the Phanerozoic in terms of the number of formations they are present in globally (A) and within their own environments (B). A, proportion of formations that contain at least one reef-building ecosystem engineer per stage; point colours correspond to period on the x-axis. B, average proportion of taxa that are reef-builders across all formations containing reef-building ecosystem engineers, with point colours representing the dominant reef-builder group in that time period; point colours correspond to reef builder groups in bottom legend. Data points are the average value of 1000 bootstrap subsampling iterations for each stage, and error bars are the 5th and 95th quantiles. Where error bars are not shown, point character size is larger than error. See Figure 1 for timescale abbreviations. Geological timescale is visualized using the R package *deepsite* (v1.1.1) (Gearty 2023).

significantly increased in their relative abundance of bio-turbating ecosystem engineers (Fig. 3).

Phanerozoic trends in reef-building

Formations preserving reef-building ecosystem engineers become more common through the early Palaeozoic, reaching a peak in the Devonian, and then declining to remain relatively stable up until the Holocene (Fig. 4). Overall, there is no strong directional trend through the entire Phanerozoic. During the Cambrian, reef-builders are present in around 8% of all fossiliferous formations, decreasing towards a reef gap during Stage 10. Between the Ordovician and end of the Devonian, the proportion of formations containing reef-builders increased through to the Frasnian, when the dominance of reef-builder

formations reached an all-Phanerozoic peak, present in $45.7 \pm 2.87\%$ of all fossiliferous formations. (Fig. 4). This dominance sharply declines into the Famennian coincident with the end-Devonian mass extinction, and broadly gradually declines through the remainder of the Phanerozoic. Following a sharp decline at the Permian–Triassic boundary concurrent with the EPME, the proportion of fossiliferous formations that contain reef-builders is dynamic but generally not directionally trending, oscillating around 15%. There are notable peaks during in the Norian in the late Triassic ($23.9 \pm 2.55\%$), Oxfordian in the Jurassic ($32.5 \pm 2.61\%$), and Holocene ($34.0 \pm 2.50\%$), and significant declines during the early Jurassic and at the Jurassic–Cretaceous boundary (Fig. 4). These trends generally follow the proportion of reef facies out of total fossiliferous formations throughout the Phanerozoic (Fig. S3). Comparing only within similar

environments, these trends of a Devonian peak and subsequent dynamic but non-trending dominance persist in most facies. Significant peaks in the Ordovician arise in shallow and deep siliciclastic facies and during the Miocene in deep carbonate facies, although this is almost certainly driven by the small number of total deep environments containing reef-builders during those intervals. Additionally, the Devonian peak is less significant in carbonates, as the proportion of carbonate fossiliferous formations are nearly as high in several intervals throughout the Mesozoic and Cenozoic (Fig. S4).

The dominance of reef-builders within their own environments follows similar but far more dynamic trends through the Phanerozoic (Fig. 4). During the Cambrian and early Ordovician, the average proportion of taxa that are reef-building ecosystem engineers across formations is particularly high during the Fortunian ($58.3 \pm 18.2\%$), Tremadocian ($45.5 \pm 23.3\%$), Dapingian ($38.1 \pm 35.1\%$), and Darriwillian ($39.6 \pm 16.2\%$), although with very high uncertainty arising from the large variance in the number of reef-builders that are present in different formations (Fig. 4). This uncertainty reflects that some reef communities are primarily composed of reef-builders and some communities are composed of other taxa preserved with only a few reef-builders. The dominance of reef-builders within their own formations rises to the Devonian, when on average over two-thirds of taxa in reef formations are reef-builders during the Eifelian, Givetian and Frasnian (Fig. 4). The dominance of reef-builders within their communities then declines towards the end of the Permian, with some increases during the middle of the Carboniferous and early Permian, but ultimately culminating in a crash at the EPME. After declining through the Permian, reef-builders only constituted less than 5% of the taxa in their formations during the Induan, although they recovered quickly to early Permian levels by the Anisian. A second significant decline occurred during the Toarcian. The remainder of the Phanerozoic has no clear upwards trend, despite notable peaks in the Berriasian ($83.8 \pm 17.5\%$), Coniacian ($75.9 \pm 7.51\%$), and Holocene ($85.6 \pm 2.41\%$). These trends are most consistent when constrained within shallow and carbonate facies, while deep and siliciclastic facies exhibit different and highly dynamic trends that most likely arise due to small sample sizes (Fig. S5). However, in no environment do we observe any strong positive or negative Phanerozoic trend in the dominance of reef-builders within their own formations (Fig. S4).

Finally, there are clear shifts in the dominant reef-builder groups through the Phanerozoic (Figs 4, 5). During the Cambrian and early Ordovician, sponge reef-builders were dominant, with archaeocyathids and glass sponges representing most reef-builders (Fig. 5). Following a reef gap during Stage 10, the rest of the Phanerozoic

is dominated by coral reef ecosystem engineers. There is a transition from sponge reef-builders to tabulate and rugose coral reef-builders through the Ordovician, Silurian and Devonian. During these periods, tabulate corals were initially dominant (reaching their acme in the Silurian) while rugose corals were on the rise. At the same time, the relative abundance of stromatoporoids increased into the Devonian. Through the rest of the Palaeozoic, rugose corals became dominant, representing most reef-builders by the end of the Permian. There is a stark shift across the Permian–Triassic boundary coincident with the EPME, where tube worms and hydrozoan reefs become briefly dominant during the Induan (reflecting patterns noted by Pruss & Bottjer (2005), Wu *et al.* (2007) and He *et al.* (2013)) followed by the rapid rise of Scleractinia for the remainder of the Phanerozoic (Fig. 5). This trend of the rise of the stony corals is only punctuated by a surge in the dominance of tube worms during the Jurassic and a surge in rudist bivalves and glass sponges at the end of the Cretaceous (Fig. 5). Unsurprisingly, nearly all reef-builders in our dataset during the Holocene are scleractinian corals.

DISCUSSION

The rise and fall of marine ecosystem engineers

In reconstructing the rise to dominance of marine ecosystem engineers through the Phanerozoic, it is clear that bioturbators and reef-building ecosystem engineers have had different trajectories over geological time. Bioturbating ecosystem engineers had a strong start in the early Cambrian, dominated by molluscan surficial grazers (Mángano & Buatois 2017) (Figs 4, 5), followed by their decline and replacement by other taxonomic and ecological groups through the Ordovician and Silurian. The strong start in the earliest stages of the Cambrian reflects the Cambrian Substrate Revolution (Bottjer *et al.* 2000). Simple, horizontal bioturbating ecosystem engineers representing grazers and deposit feeders were already on the rise in the late Ediacaran, adapted to microbial-mat rich food sources (Herringshaw *et al.* 2017; Mángano & Buatois 2017; Cribb *et al.* 2019; Darroch *et al.* 2021). As these microbial matgrounds persisted into the early Cambrian (Buatois *et al.* 2014), as did these grazing and deposit feeding ecosystem engineers and their presence in a high number of local communities. However, as benthic food sources changed due to the decline of microbial mats (perhaps, in part, due to the bioturbating ecosystem engineers themselves; Bottjer *et al.* 2000) these ecosystem engineers also began to decline (Fig. 1) and ecological strategies shifted (Fig. 4). Importantly, our data suggest that bioturbating ecosystem engineers in the

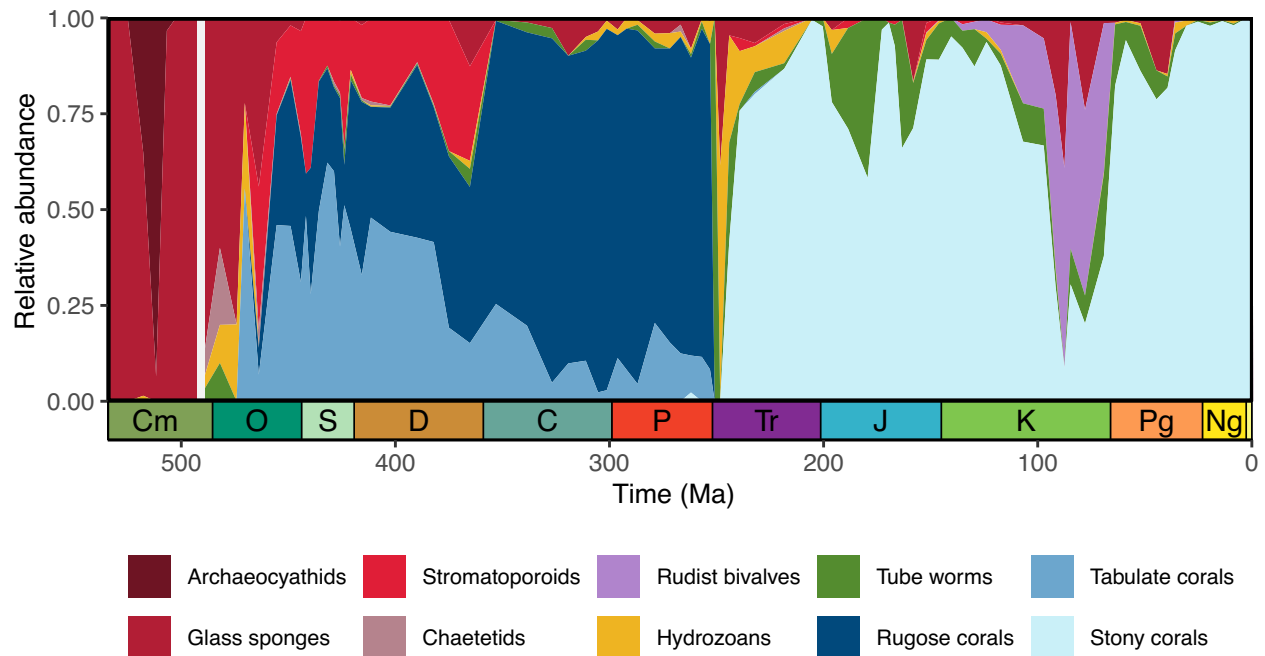


FIG. 5. Relative abundance of reef-building ecosystem engineer groups over the Phanerozoic. Ribbon colours correspond to the 10 reef-builder groups in the bottom legend. Grey bar at the end of the Cambrian represents a reef gap that occurs in Stage 10. Data shown are the average of 1000 bootstrap subsampling iterations for each stage. See Figure 1 for timescale abbreviations. Geological timescale is visualized using the R package *deptime* (v1.1.1) (Gearty 2023).

Cambrian were not as dominant within their own communities as bioturbators were pervasive in different communities.

The number of formations possessing bioturbators began rising in the Carboniferous, while the dominance of bioturbators within these formations began to rise slightly earlier, during the Devonian. That bioturbating ecosystem engineers begin to appear in an increasingly higher proportion of formations through the Palaeozoic probably reflects an increase in environments that are habitable for bioturbating ecosystem engineers. Given a concurrent shift to a greater relative abundance of suspension feeders over grazers (Figs 1, 2), this may reflect changes in benthic food sources associated with changes in the biological pump and food webs (Bambach 1993). The dominance of bioturbating ecosystem engineers would have then been further fuelled by the Mesozoic Marine Revolution (MMR), which saw a shift to modern-style bioturbating behaviours and taxa as benthic prey developed better burrowing defence strategies (Vermeij 1977; Tackett & Bottjer 2012; Buatois & Mángano 2018). The continued increase in dominance of bioturbators through to the Holocene suggests that they may have engineered their own continued success. As the deep-tier and intense-reworking burrowing behaviours were selected for during the MMR, these ecosystem engineers may have triggered their own positive feedback loop

(Jones *et al.* 2010), stimulating nutrient cycling and increased resource availability for other organisms in their environments, and in turn supporting even stronger and more effective burrowing behaviours (McIlroy & Logan 1999). Finally, while there were significant decreases in the proportion of communities impacted by bioturbating ecosystem engineers around mass extinctions and hyperthermal events in the Mesozoic (Fig. 1), these were not catastrophic in the sense that bioturbator-influenced communities became especially rare. Moreover, there were no major impacts to the dominance of bioturbators within their own communities across warming-driven extinction events like the end-Permian or end-Triassic mass extinctions (Fig. 1). This is perhaps surprising given previous observations about the severe effects of mass extinctions on bioturbator activities (e.g. Hofmann *et al.* 2015), although previous work has documented the persistence and resilience of bioturbators in the wake of the EPME (Cribb & Bottjer 2020; Feng *et al.* 2022). Given that ecosystem engineers are effective at ameliorating environmental stress (Byers *et al.* 2006), bioturbators may have been able to engineer their own refugia and maintain resource availability in spite of climate-related stressors, buffering them from the strong effects of mass extinction events.

Meanwhile, reef-building ecosystem engineers did not experience as strong a rise to dominance through the

Phanerozoic. Reef-builder influenced communities were relatively common in the early Cambrian compared to their Ordovician counterparts, with high but very dynamic dominance within their own communities (Fig. 4). Cambrian reef-building ecosystem engineers were sponges, primarily hexactinellids, with archaeocyathids comprising significant proportions during Stage 3 and Stage 4. These sponge reefs would have been vital ecosystem engineers, ventilating the water columns through passive and active suspension feeding (Pratt *et al.* 2000; Gibson *et al.* 2023), and building an early global sponge pump that would have been a major component of carbon and silica cycling (Erwin & Tweedt 2011). However, we note that the strength of sponge pump impacts would have been a function of body size (Aragónés Suarez & Leys 2022). Reef-building ecosystem engineers are most dominant during the cool middle Devonian (Joachimski *et al.* 2009), both in terms of how common reef ecosystem engineered-environments were, and how common reef-builders were in their own environments. After the reef collapse coincident with the Late Devonian mass extinction, reef-builders never regain their prior dominance in terms of how many communities they influence, but they do become more dominant within their own communities at times during the Mesozoic and Cenozoic (Fig. 4). Following the EPME and the associated coral reef gap, when hydrozoan and tube worms were dominant in the Induan, modern-type scleractinian corals rapidly rose to dominance (Kiessling & Flügel 2002) (Figs 4, 5). However, the rise of stony corals is not associated with an upward trend in dominance, and the Mesozoic and Cenozoic trends in the dominance of reef-builders across formations and within their own communities is highly dynamic and subject to numerous significant declines (Fig. 4). Despite the strong ecosystem engineering effect of scleractinian corals today in creating biodiversity hotspots, this trend may reflect the environmental sensitivity of scleractinians and their inability to establish resilient reef-environments in the Mesozoic and Early Cenozoic hothouse climates (Scotese *et al.* 2021). Relatedly, reef-builders clearly lose dominance associated with the end-Permian and end-Triassic mass extinctions, and Toarcian Ocean Anoxia Event (Fig. 4), reflecting the suppression of reef-building ecosystem engineers by rapid climate warming events (Wild *et al.* 2011).

Ecosystem engineering regime shifts

Our results suggest the presence of distinct ecosystem engineering regimes, and regime shifts, throughout the Phanerozoic associated with the rise and fall of different behaviours and groups. For bioturbating ecosystem engineers, these regime shifts occur most clearly with changes

in dominant feeding modes. The first Phanerozoic bioturbating ecosystem engineering regime is present in the Cambrian, characterized by the grazers that were initially present in a high proportion of environments, broadly reflecting the Cambrian Evolutionary Fauna (Sepkoski 1981). It has been noted that these small, surficial grazing bioturbators had minimal impact on substrate rheology and biogeochemical cycling of key nutrients (Tarhan *et al.* 2015; Tarhan 2018; Cribb *et al.* 2023) despite the presence of complex small ecosystem engineering behaviours that evolved in the Ediacaran (Cribb *et al.* 2019; Darroch *et al.* 2021). Therefore, this was most likely an initially weak ecosystem engineering regime in comparison to those that follow. This Cambrian regime would have been relatively ecologically similar to the Ediacaran, when surficial deposit feeding and grazing trace fossils were most common (Mángano & Buatois 2020; Cribb *et al.* 2023). Future research integrating global Ediacaran body fossil datasets with Phanerozoic PBDB data will be useful to quantify how similar Ediacaran bioturbating ecosystem engineers were to their Cambrian successors.

Within the Palaeozoic Evolutionary Fauna (Sepkoski 1981), a second bioturbating ecosystem engineering regime can perhaps be identified between the late Cambrian and end of the Silurian, when grazing bioturbators decline and suspension feeders and deposit feeders become more abundant with the rise of brachiopods and arthropods (Figs 2, 3). Although bioturbation was still relatively weak in terms of sediment reworking and mixed layer development during this time interval (Tarhan 2018), this shift away from grazing would have had major consequences for bioturbators' ecosystem engineering impacts. A rise in suspension feeding would have caused stronger ventilation of the water column and oxygenation of the seafloor, while the rise in deposit feeding would have caused greater recycling of key nutrients such as organic matter and phosphorus (van de Velde *et al.* 2018; Tarhan *et al.* 2021; Cribb *et al.* 2023). A third ecosystem engineering regime follows between the Devonian and Permian, with a second rise of grazing bioturbators and a sustained dominance of suspension feeders (Fig. 2). This ecosystem engineering regime represents relatively diverse ecosystem engineering behaviours and processes, as suspension feeders, deposit feeders, and surficial grazers together would likely have resulted in differential impacts to benthic nutrient cycling, substrate characteristics, and resource availability. Given the diversity of these behaviours, bioturbation ecosystem engineering in this third regime probably resulted in significant habitat heterogeneity, thus potentially driving increased biodiversity on the seafloor (Erwin 2008).

Reflecting the Modern Evolutionary Fauna (Sepkoski 1981), a fourth bioturbation ecosystem engineering

regime is observed at the onset of the Mesozoic and persists during the Triassic and Jurassic. This regime is characterized by the dominance of suspension feeders (Figs 1, 2) and a shift in which arthropods became a smaller component of bioturbating taxa, while echinoderms gradually became more common, and molluscs remained the dominant bioturbating group (Fig. 3). At the start of the Cretaceous and persisting through the remainder of the Phanerozoic, a final regime arose as deposit feeders (Fig. 2) and echinoderms (Fig. 3) gained dominance. Although suspension feeders were still dominant, the greater evenness in feeding ecologies during this final regime are likely to have contributed to a higher degree of habitat heterogeneity and, potentially, a higher degree of geographic provincialism associated with unique ecosystem engineering assemblages. The onset of these final regimes corresponds to start of the MMR, which saw the rise of intense and modern-type bioturbation behaviours that are characterized by deeper, more complex infaunal burrowing (Buatois & Mángano 2018). These final bioturbating ecosystem engineers (both environmentally pervasive and dominant in their own communities) are likely to have exerted even stronger impacts on their benthic environments than previously in the Phanerozoic.

Reef-building ecosystem engineers also exhibit clear regime shifts that strongly reflect the Cambrian, Palaeozoic, and Modern Evolutionary Faunas (Sepkoski 1981). The first Phanerozoic reef-building ecosystem engineering regime was dominantly built by glass sponges, with archaeocyathids briefly rising to prominence between Cambrian Stage 3 and Stage 4 (Figs 4, 5). Cambrian sponge reef-builders have been noted to have been high-tiering reefs, reaching tens of centimetres off of the seafloor (Yuan *et al.* 2002; Wu *et al.* 2014), and thus would have been important for establishing ecosystem complexity and opening new ecospace (Ausich & Bottjer 1982; Erwin *et al.* 2011). Furthermore, sponge reef-builders' topographic relief above the seafloor may have contributed to controls on hydrodynamic flow in their habitats, which is a major effect of reef ecosystem engineering (Jones *et al.* 1994; Monismith 2007; Davis *et al.* 2021). Archaeocyathids in particular are likely to have been significant ecosystem engineers during Stage 3 and Stage 4, not only as effective active suspension feeders (Gibson *et al.* 2023), but also in creating significant physical heterogeneity on the seafloor and creating expansive reef area (Manzuk *et al.* 2023).

The subsequent gradual transition to a second ecosystem engineering regime between the Ordovician and Permian broadly reflects the Palaeozoic Evolutionary Fauna (Sepkoski 1981). This regime is characterized by the rise of tabulate and rugose corals. Sponge reefs persisted, but now dominantly constructed by stromatoporoids, as archaeocyathids went extinct and glass sponges became

rare (Fig. 5). The initial turnover in this regime to tabulate corals may have been significant for facilitating the rise of reef-building ecosystem engineers through the Devonian (Dhungana & Mitchell 2021). This Devonian peak in reef-building ecosystem engineering dominance is most likely to have been the result of high diversity in metazoan reef-builders during this interval, reflected in the relatively even proportions of stromatoporoids, rugose corals and tabulate corals (Figs 4, 5). If stromatoporoids, rugose corals and tabulate corals had different environmental preferences and climatic tolerances, this would allow reef-building ecosystem engineers to proliferate into a variety of habitats across the oceans. Moreover, this would have contributed to an increase in environmental heterogeneity as different reef-builders create new types of reef structures, thus allowing for increases in biodiversity as resource availability and habitat differentiation increased. This would have been particularly impactful if stromatoporoids, rugose corals and tabulate corals possessed a range of different ecosystem engineering impacts, although this remains unresolved. The fall in reef-builder dominance coincided with rise of rugose corals, as stromatoporoids disappeared and tabulate corals significantly declined. This fall in reef dominance was likely to have been driven by environmental factors (Joachimski *et al.* 2009; Kiessling 2009), but may also reflect a reduction in viable marine habitat space as the environmental tolerance of reef-building ecosystem engineers would have been almost exclusively a function of a single reef-building group (rugose corals) by the end of the Carboniferous (Fig. 5). We note that if tabulate and rugose corals did have significantly different ecosystem engineering effects, this regime may more be appropriately divided into a tabulate coral- and stromatoporoid-dominated regime and a rugose coral-dominated regime near the Devonian–Carboniferous boundary.

Finally, a third reef-building ecosystem engineering regime appears in the Triassic and persists for the remainder of the Phanerozoic, reflecting the rise of the Modern Evolutionary Fauna (Sepkoski 1981). There is a gap between the second and third reef ecosystem engineering regimes that reflect the EPME and subsequent 'coral reef gap' (Kiessling 2009; Martindale *et al.* 2019). In the earliest Triassic stages following the extinction, hydrozoans, glass sponges and tube worms occupied the role of reef-builders, but quickly lost dominance as ecosystems recovered in the wake of the EPME. Most significantly, this regime sees the evolution of modern-type coral reef-building ecosystem engineering with the rapid rise and prolonged dominance of scleractinian corals. The dominance of these 'true reef' ecosystem engineers would have created the uniquely complex reef habitats that host biodiversity hotspots today (Jones *et al.* 1994; Wild *et al.* 2011). While other reefs have been shown to have

functioned as evolutionary cradles earlier in the Phanerozoic (Kiessling *et al.* 2010), the complexity associated with three-dimensional reef structures and elevated nutrient cycling associated with scleractinian corals (Jones *et al.* 1994; Wild *et al.* 2011) are likely to have made them uniquely powerful ecosystem engineers. During the Mesozoic, this regime also occasionally sees the loss of scleractinian coral dominance, giving way to tube worm and bivalve reef-builders (and coinciding with mass extinctions and ocean anoxic events) (Fig. 5). Given the turnover to non-coral reef-builders, these intervals probably represent rapid shifts between entirely new ecosystem engineering modes.

Finally, there is a Holocene peak in reef dominance when scleractinian corals represent the vast majority of reef-building ecosystem engineers (Figs 4, 5). Despite their strength, this lack of redundancy in reef-builder ecosystem engineering groups highlights our current state of vulnerability in losing reef-hosted biodiversity hotspots. Without a diverse group of reef-building ecosystem engineers in our oceans, as has been present for the majority of the Phanerozoic, the loss of scleractinian coral reefs may see another future coral reef gap. As occurred in the wake of the EPME, this may be followed by a turnover to an entirely new reef-building ecosystem engineering regime, threatening the maintenance of our marine biodiversity hotspots on geological timescales.

Abundance versus impact in ecosystem engineering on geological timescales

Our study quantifies changes in the proportion of environments and communities possessing reef-building and bioturbating ecosystem engineers through time. However, clear mechanistic links between the rise of these ecosystem engineers and changes in ecology and biodiversity in their communities are yet to be drawn. In this context, a crucial question is: to what extent did the changes in ecosystem engineering abundance and ecologies documented here lead to more habitable environments that could host greater marine biodiversity? In theory, the 'strength' of an ecosystem engineer depends on three factors: the intensity and effectiveness of the behaviour, the abundance of taxa that perform that behaviour, and the potential for co-existing organisms to be impacted by the environmental changes arising from those behaviours. These factors are unlikely to always be linear. Consider, for example, the 'complex' ecosystem engineering behaviours in the form of deep network burrowing that locally persist in the wake of the EPME (Cribb & Bottjer 2020; Feng *et al.* 2022), represented here by the persistence of bioturbator dominance across the Permian–Triassic boundary (Fig. 1). Although the persistence of burrowing

behaviours with complex vertical components might be expected to have strong ecosystem engineering impacts, it remains unclear what the precise ecological impacts of these behaviours were in the context of potentially creating and maintaining Early Triassic refugia. While these complex bioturbation ecosystem engineering behaviours have been linked with stimulated nutrient recycling (Cribb & Bottjer 2020), more recent work has highlighted the extremely environmentally-dependent effects of bioturbators as modulators of nutrient cycling (van de Velde *et al.* 2021; Cribb *et al.* 2023). Similarly, the collapse of the Early Triassic mixed layer depth (Hofmann *et al.* 2015) may have in reality had little ecological consequence in the context of catastrophic physiologically-driven extinction (Penn *et al.* 2018), which would have acted as the primary extrinsic driver of ecosystem collapse and suppressed recovery. There is, therefore, a crucial missing link between ecosystem engineering abundance and impact: the environmental context in which the community exists. While this study quantifies the changing proportion of different ecosystem engineering processes through the Phanerozoic, there is substantial work still to be done in linking these processes with their consequences for biodiversity.

CONCLUSION

The evolutionary history of ecosystem engineers is a major yet underexplored aspect of what has driven changes in biodiversity over the course of Earth history. Focusing specifically on marine bioturbation and reef-building, we have identified unique temporal trends in different groups of ecosystem engineers. While bioturbators have experienced a continuous upward trend for the majority of the Phanerozoic, reef-builders reached their peak in the early Devonian and have shown little overall change since the Triassic. Unique ecosystem engineering regimes seem to exist for both bioturbators and reef-builders, which broadly reflect the Cambrian, Palaeozoic and Modern Evolutionary Faunas. This would suggest that major evolutionary intervals that are known to trigger profound taxonomic and ecological restructuring, such as evolutionary radiations and extinction events, can also trigger the rise of new ecosystem engineering processes and outcomes. Unsurprisingly, the present-day modes of marine ecosystem engineering seem to have evolved in the Mesozoic and persisted until the present day. Future work is needed to determine the spectrum and strength of impacts for groups of ancient ecosystem engineers (particularly in reef-building groups). Overall, these results shed new light on how the pervasiveness, dominance, and ecology of ecosystem engineering behaviours have changed through time, and they will be

important for linking ecosystem engineering to the changes in biodiversity over the course of Earth history.

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DATA ARCHIVING STATEMENT

Data for this study are available in the GitHub Repository: <https://github.com/atcribb/Rise-of-the-Ecosystem-Engineers>. This repository contains the full Phanerozoic fossil dataset, bioturbators dataset, and reef-builders dataset, the R scripts needed to reproduce each analysis in the paper, the output files used as the results for this paper, and the R scripts needed to produce the main text and supplemental figures.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12726>):

Figure S1. Dominance of formations containing bioturbators within specific palaeoenvironments.

Figure S2. Dominance of bioturbators within their own communities in specific environments.

Figure S3. Changes in reef facies through the Phanerozoic.

Figure S4. Dominance of formations containing reef-builders within specific palaeoenvironments.

Figure S5. Dominance of reef-builders within their own communities in specific palaeoenvironments.

Appendix S1. List of contributors to the PBDB whose data were included in this study.

REFERENCES

Albertson, L. K., Sklar, L. S., Tumolo, B. B., Cross, W. F., Collins, S. F. and Woods, H. A. 2024. The ghosts of ecosystem

engineers: legacy effects of biogenic modifications. *Functional Ecology*, **38**, 52–72.

Allwood, A. C., Walter, M. R., Kamber, B. S., Marshall, C. P. and Burch, I. W. 2006. Stromatolite reef from the Early Archaean era of Australia. *Nature*, **441**, 714–718.

Alroy, J. 2008. Dynamics of origination and extinction in the marine fossil record. *Proceedings of the National Academy of Sciences*, **105**, 11536–11542.

Aragónés Suarez, P. and Leys, S. P. 2022. The sponge pump as a morphological character in the fossil record. *Paleobiology*, **48**, 446–461.

Ausich, W. I. and Bottjer, D. J. 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science*, **216**, 173–174.

Bambach, R. K. 1993. Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology*, **19**, 372–397.

Berke, S. K. 2010. Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integrative & Comparative Biology*, **50**, 147–157.

Bottjer, D. J., Hagadorn, J. W. and Dornbos, S. Q. 2000. The Cambrian substrate revolution. *GSA Today*, **10**, 1–7.

Buatois, L. A. and Mángano, M. G. 2018. The other biodiversity record: innovations in animal-substrate interactions through geologic time. *GSA Today*, **28**, 4–10.

Buatois, L. A., Narbonne, G. M., Mángano, M. G., Carmona, N. B. and Myrow, P. 2014. Ediacaran matground ecology persisted into the earliest Cambrian. *Nature Communications*, **5**, 1–5.

Butterfield, N. J. 2011. Animals and the invention of the Phanerozoic Earth system. *Trends in Ecology & Evolution*, **26**, 81–87.

Byers, J. E., Cuddington, K., Jones, C. G., Talley, T. S., Hastings, A., Lambrinos, J. G., Crooks, J. A. and Wilson, W. G. 2006. Using ecosystem engineers to restore ecological systems. *Trends in Ecology & Evolution*, **21**, 493–500.

Cheung, P., Nozawa, Y. and Miki, T. 2021. Ecosystem engineering structures facilitate ecological resilience: a coral reef model. *Ecological Research*, **36**, 673–685.

Cribb, A. T. and Bottjer, D. J. 2020. Complex marine bioturbation ecosystem engineering behaviors persisted in the wake of the end-Permian mass extinction. *Scientific Reports*, **10**, 1–8.

Cribb, A. T., Kenchington, C. G., Koester, B., Gibson, B. M., Boag, T. H., Racicot, R. A., Mocke, H., Laflamme, M. and Darroch, S. A. F. 2019. Increase in metazoan ecosystem engineering prior to the Ediacaran–Cambrian boundary in the Nama Group, Namibia. *Royal Society Open Science*, **6**, 190548.

Cribb, A. T., Van De Velde, S. J., Berelson, W. M., Bottjer, D. J. and Corsetti, F. A. 2023. Ediacaran–Cambrian bioturbation did not extensively oxygenate sediments in shallow marine ecosystems. *Geobiology*, **21**, 435–453.

Darroch, S. A. F., Cribb, A. T., Buatois, L. A., Germs, G. J. B., Kenchington, C. G., Smith, E. F., Mocke, H., O’Neil, G. R., Schiffbauer, J. D., Maloney, K. M., Racicot, R. A., Turk, K. A., Gibson, B. M., Almond, J., Koester, B., Boag, T. H., Tweedt, S. M. and Laflamme, M. 2021. The trace fossil record of the Nama Group, Namibia: exploring the terminal Ediacaran roots of the Cambrian explosion. *Earth-Science Reviews*, **212**, 103435.

- Davis, E. B. 2005. Mammalian beta diversity in the Great Basin, western USA: palaeontological data suggest deep origin of modern macroecological structure. *Global Ecology & Biogeography*, **14**, 479–490.
- Davis, K. A., Pawlak, G. and Monismith, S. G. 2021. Turbulence and coral reefs. *Annual Review of Marine Science*, **13**, 343–373.
- Dhungana, A. and Mitchell, E. G. 2021. Facilitating corals in an early Silurian deep-water assemblage. *Palaeontology*, **64**, 359–370.
- Erwin, D. H. 2008. Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology & Evolution*, **23**, 304–310.
- Erwin, D. H. and Tweedt, S. M. 2011. Ecosystem engineering and the Ediacaran-Ordovician diversification of Metazoa. *Evolutionary Ecology*, **26**, 417–433.
- Erwin, D. H., Laflamme, M., Tweedt, S. M., Sperling, E. A., Pisani, D. and Peterson, K. J. 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science*, **334**, 1091–1097.
- Feng, X., Chen, Z.-Q., Benton, M. J., Su, C., Bottjer, D. J., Cribb, A. T., Li, Z., Zhao, L., Zhu, G., Huang, Y. and Guo, Z. 2022. Resilience of infaunal ecosystems during the Early Triassic greenhouse Earth. *Science Advances*, **8**, eabo0597.
- Gearty, W. 2023. deeptime. v1.1.1. <https://williamgearty.com/deeptime/>
- Gibson, B. M., Chipman, M., Attanasio, P., Qureshi, Z., Darroch, S. A. F., Rahman, I. A. and Laflamme, M. 2023. Reconstructing the feeding ecology of Cambrian sponge reefs: the case for active suspension feeding in Archaeocyatha. *Royal Society Open Science*, **10**, 230766.
- Guy-Haim, T., Lyons, D. A., Kotta, J., Ojaveer, H., Queirós, A. M., Chatzinikolaou, E., Arvanitidis, C., Como, S., Magni, P., Blight, A. J., Orav-Kotta, H., Somerfield, P. J., Crowe, T. P. and Rilov, G. 2018. Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: a global review and meta-analysis. *Global Change Biology*, **24**, 906–924.
- Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S. and Wilson, W. G. 2007. Ecosystem engineering in space and time. *Ecology Letters*, **10**, 153–164.
- He, L., Wang, Y., Woods, A., Li, G., Yang, H. and Liao, W. 2013. Calcareous tubeworms as disaster forms after the end-Permian mass extinction in South China. *Palaos*, **27**, 878–886.
- Heim, N. A. and Peters, S. E. 2011. Covariation in macrostratigraphic and macroevolutionary patterns in the marine record of North America. *Geological Society of America Bulletin*, **123**, 620–630.
- Herringshaw, L. G., Callow, R. H. T. and McIlroy, D. 2017. Engineering the Cambrian explosion: the earliest bioturbators as ecosystem engineers. *Geological Society, London, Special Publications*, **448**, 369–382.
- Hofmann, R., Buatois, L. A., MacNaughton, R. B. and Mángano, M. G. 2015. Loss of the sedimentary mixed layer as a result of the end-Permian extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **428**, 1–11.
- Joachimski, M. M., Breisig, S., Buggisch, W., Talent, J. A., Mawson, R., Gereke, M., Morrow, J. R., Day, J. and Weddige, K. 2009. Devonian climate and reef evolution: insights from oxygen isotopes in apatite. *Earth & Planetary Science Letters*, **284**, 599–609.
- Jones, C. G., Lawton, J. H. and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos*, **69**, 373.
- Jones, C. G., Gutiérrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G. and Talley, T. S. 2010. A framework for understanding physical ecosystem engineering by organisms. *Oikos*, **119**, 1862–1869.
- Kiessling, W. 2002. Secular variations in the Phanerozoic reef ecosystem. 625–690. In Kiessling, W., Flügel, E. and Golonka, J. (eds) *Phanerozoic reef patterns*. Society for Sedimentary Geology. SEPM Special Publication, 72.
- Kiessling, W. 2009. Geologic and biologic controls on the evolution of reefs. *Annual Review of Ecology, Evolution, & Systematics*, **40**, 173–192.
- Kiessling, W. and Flügel, E. 2002. Paleoreefs—a database on Phanerozoic reefs. 77–92. In Kiessling, W., Flügel, E. and Golonka, J. (eds) *Phanerozoic reef patterns*. Society for Sedimentary Geology. SEPM Special Publication, 72.
- Kiessling, W., Simpson, C. and Foote, M. 2010. Reefs as cradles of evolution and sources of biodiversity in the Phanerozoic. *Science*, **327**, 196–198.
- Kocsis, Á. T., Reddin, C. J., Alroy, J. and Kiessling, W. 2019. The R package divDyn for quantifying diversity dynamics using fossil sampling data. *Methods in Ecology & Evolution*, **10**, 735–743.
- Kristensen, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Life at Interfaces & Under Extreme Conditions*, **426**, 1–24.
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. and Banta, G. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, **446**, 285–302.
- Lovelock, J. E. 1972. Gaia as seen through the atmosphere. *Atmospheric Environment* (1967), **6**, 579–580.
- Lovelock, J. E. 1995. *The ages of Gaia: A biography of our living Earth*. Norton.
- Lovelock, J. E. and Margulis, L. 1974. Atmospheric homeostasis by and for the biosphere: the Gaia hypothesis. *Tellus*, **26**, 2–10.
- Mángano, M. G. and Buatois, L. A. 2017. The Cambrian revolutions: trace-fossil record, timing, links and geobiological impact. *Earth-Science Reviews*, **173**, 96–108.
- Mángano, M. G. and Buatois, L. A. 2020. The rise and early evolution of animals: where do we stand from a trace-fossil perspective? *Interface Focus*, **10**, 20190103.
- Manzuk, R. A., Maloof, A. C., Kaandorp, J. A. and Webster, M. 2023. Branching archaeocyaths as ecosystem engineers during the Cambrian radiation. *Geobiology*, **21**, 66–85.
- Martindale, R. C., Foster, W. J. and Velledits, F. 2019. The survival, recovery, and diversification of metazoan reef ecosystems following the end-Permian mass extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **513**, 100–115.
- McIlroy, D. and Logan, G. A. 1999. The impact of bioturbation on infaunal ecology and evolution during the Proterozoic-Cambrian transition. *Palaos*, **14**, 58–72.

- Meysman, F. J. R., Middelburg, J. J. and Heip, C. H. R. 2006. Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology & Evolution*, **21**, 688–695.
- Minter, N. J., Buatois, L. A., Mángano, M. G., Davies, N. S., Gibling, M. R., Macnaughton, R. B. and Labandeira, C. C. 2017. Early bursts of diversification defined the faunal colonization of land. *Nature Ecology & Evolution*, **1**, 0175.
- Monismith, S. G. 2007. Hydrodynamics of coral reefs. *Annual Review of Fluid Mechanics*, **39**, 37–55.
- Morris, J. L., Leake, J. R., Stein, W. E., Berry, C. M., Marshall, J. E. A., Wellman, C. H., Milton, J. A., Hillier, S., Mannolini, F., Quirk, J. and Beerling, D. J. 2015. Investigating Devonian trees as geo-engineers of past climates: linking palaeosols to palaeobotany and experimental geobiology. *Palaeontology*, **58**, 787–801.
- Penn, J. L., Deutsch, C., Payne, J. L. and Sperling, E. A. 2018. Temperature-dependent hypoxia explains biogeography and severity of end-Permian marine mass extinction. *Science*, **362**, eaat1327.
- Penny, A. M., Wood, R., Curtis, A., Bowyer, F., Tostevin, R. and Hoffman, K. H. 2014. Ediacaran metazoan reefs from the Nama Group, Namibia. *Science*, **344**, 1504–1506.
- Pratt, B. R., Spincer, B. R., Wood, R. A. and Zhuravlev, A. Y. 2000. Ecology and evolution of Cambrian reefs. 254–274. In Zhuravlev, A. and Riding, R. (eds) *The ecology of the Cambrian radiation*. Columbia University Press.
- Pruss, S. B. and Bottjer, D. J. 2005. The reorganization of reef communities following the end-Permian mass extinction. *Comptes Rendus Palevol*, **4**, 553–568.
- Reichman, O. and Seabloom, E. W. 2002. Ecosystem engineering: a trivialized concept? *Trends in Ecology & Evolution*, **17**, 308.
- Romero, G. Q., Gonçalves-Souza, T., Vieira, C. and Koricheva, J. 2015. Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*, **90**, 877–890.
- Scotese, C. R., Song, H., Mills, B. J. W. and van der Meer, D. G. 2021. Phanerozoic paleotemperatures: the earth's changing climate during the last 540 million years. *Earth-Science Reviews*, **215**, 103503.
- Sebens, K. P., Grace, S. P., Helmuth, B., Maney, E. J. Jr and Miles, J. S. 1998. Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites*, in a field enclosure. *Marine Biology*, **131**, 347–360.
- Sepkoski, J. J. Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, **7**, 36–53.
- Smiley, T. M., Bahadori, A., Rasbury, E. T., Holt, W. E. and Badgley, C. 2024. Tectonic extension and paleoelevation influence mammalian diversity dynamics in the Basin and Range Province of western North America. *Science Advances*, **10**, eadn6842.
- Stanley, S. M. 2006. Influence of seawater chemistry on biomineralization throughout phanerozoic time: paleontological and experimental evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 214–236.
- Tackett, L. S. and Bottjer, D. J. 2012. Faunal succession of Norian (Late Triassic) level-bottom benthos in the Lombardian basin: implications for the timing, rate, and nature of the early Mesozoic Marine Revolution. *Palaos*, **27**, 585–593.
- Tarhan, L. G. 2018. The early Paleozoic development of bioturbation—evolutionary and geobiological consequences. *Earth-Science Reviews*, **178**, 177–207.
- Tarhan, L. G., Droser, M. L., Planavsky, N. J. and Johnston, D. T. 2015. Protracted development of bioturbation through the early Palaeozoic Era. *Nature Geoscience*, **8**, 865–869.
- Tarhan, L. G., Zhao, M. and Planavsky, N. J. 2021. Bioturbation feedbacks on the phosphorus cycle. *Earth & Planetary Science Letters*, **566**, 116961.
- Trepel, J., Le Roux, E., Abraham, A. J., Buitenwerf, R., Kamp, J., Kristensen, J. A., Tietje, M., Lundgren, E. J. and Svenning, J.-C. 2024. Meta-analysis shows that wild large herbivores shape ecosystem properties and promote spatial heterogeneity. *Nature Ecology & Evolution*, **8**, 705–716.
- van de Velde, S. and Meysman, F. J. R. 2016. The influence of bioturbation on iron and sulphur cycling in marine sediments: a model analysis. *Aquatic Geochemistry*, **22**, 469–504.
- van de Velde, S. J., Mills, B. J. W., Meysman, F. J. R., Lenton, T. M. and Poulton, S. W. 2018. Early Palaeozoic ocean anoxia and global warming driven by the evolution of shallow burrowing. *Nature Communications*, **9**, 2554.
- van de Velde, S. J., Hidalgo-Martinez, S., Callebaut, I., Antler, G., James, R. K., Leermakers, M. and Meysman, F. J. R. 2020. Burrowing fauna mediate alternative stable states in the redox cycling of salt marsh sediments. *Geochimica et Cosmochimica Acta*, **276**, 31–49.
- van de Velde, S. J., James, R. K., Callebaut, I., Hidalgo-Martinez, S. and Meysman, F. J. R. 2021. Bioturbation has a limited effect on phosphorus burial in salt marsh sediments. *Biogeosciences*, **18**, 1451–1461.
- Vermeij, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**, 245–258.
- Wild, C., Hoegh-Guldberg, O., Naumann, M. S., Colombo-Pallotta, M. F., Ateweberhan, M., Fitt, W. K., Iglesias-Prieto, R., Palmer, C., Bythell, J. C., Ortiz, J. C., Loya, Y. and van Woesik, R. 2011. Climate change impedes scleractinian corals as primary reef ecosystem engineers. *Marine & Freshwater Research*, **62**, 205–215.
- Wood, R. 1993. Nutrients, predation and the history of reef-building. *Palaos*, **8**, 526.
- Wood, R. and Erwin, D. H. 2018. Innovation not recovery: dynamic redox promotes metazoan radiations. *Biological Reviews*, **93**, 863–873.
- Wu, Y., Fan, J., Jiang, H. and Yang, W. 2007. Extinction pattern of reef ecosystems in latest Permian. *Chinese Science Bulletin*, **52**, 512–520.
- Wu, W., Zhu, M. and Steiner, M. 2014. Composition and tiering of the Cambrian sponge communities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **398**, 86–96.
- Yuan, X., Xiao, S., Parsley, R. L., Zhou, C., Chen, Z. and Hu, J. 2002. Towering sponges in an Early Cambrian Lagerstätte: disparity between nonbilateral and bilateral epifaunal tierers at the Neoproterozoic-Cambrian transition. *Geology*, **30**, 363–366.