







REVIEW ARTICLE

Bioturbators as ecosystem engineers in space and time

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Typescript received 11 April 2024; accepted in revised form 8 October 2024

Abstract: Biogenic sedimentary structures offer a unique perspective for understanding the role of the biosphere in the interaction with other Earth subsystems and the building up of our planet. The record of their ancient equivalents provides a wealth of information for reconstructing the role of bioturbators as ecosystem engineers using multiple ichnological proxies and methods. In this study, we present an overview of how bioturbation has worked across a broad range of spatial and temporal scales from the perspective of ecosystem engineering. Comprehensive and systematic datasets allow analyses at regional and global spatial extents, and especially over long temporal scales where sampling intensity and rock record biases can be considered. Our results underscore the significance of the Cambrian Explosion in the establishment of modern-style shallow marine ecosystems and of the Ordovician Radiation for their deep marine counterparts, as well as the continuous ecosystem impact of bioturbation during

Palaeozoic terrestrialization. Comparable datasets for the rest of the Phanerozoic have not yet been compiled. However, preliminary information indicates that colonization of ultra-deep tiers, the rise to prominence of regenerators, increased burrowing efficiency, and increased compartmentalization of the endobenthic ecospace, were products of the Mesozoic Marine Revolution. The trace-fossil record offers hard data to evaluate bioturbation as a driving force in ecosystem re-structuring and as a key factor in geobiological cycles. Models assessing these fundamental issues should be rooted empirically at different scales, from both autoecological and synecological to macroecological, making the best possible use of the rich and rapidly developing ichnological toolbox.

Key words: bioturbation, ecosystem engineering, evolutionary palaeoecology, ichnology, trace fossil, evolutionary radiation.

ECOSYSTEM engineers modify, maintain, and create habitats, changing their environment in an active fashion by directly or indirectly impacting the availability of resources to other organisms in terms of their quality, quantity, and distribution (Jones *et al.* 1994; Berkenbusch & Rowden 2003; Gilad *et al.* 2004; Wright & Jones 2006; Erwin 2008, 2024; Cuddington *et al.* 2009; Jones 2012; Kristensen *et al.* 2012; Lavelle *et al.* 2016; Emery-Butcher *et al.* 2020; Albertson *et al.* 2024). Ecosystem engineers are traditionally classified into autogenic (those that change the environment via their own living and dead tissues) and allogenic (those that perform this activity by transforming living or non-living materials through mechanical or other means) (Jones *et al.* 1994). A related concept, niche construction, deals with the fact that organisms modify their own environment by defining, creating, and destroying it in a way that is evolutionarily and ecologically consequential, changing not only conditions for other species, but creating their own conditions

of existence (Odling-Smee *et al.* 1996; Scott-Phillips *et al.* 2014; Laland *et al.* 2016; Lala 2024). Also, some of the changes caused by ecosystem engineers can persist beyond their presence, a phenomenon referred to as ecosystem engineering legacy effects (Hastings *et al.* 2007; Albertson *et al.* 2024). Effects can also be magnified by the fact that some of the recipient taxa may be ecosystem engineers as well, resulting in a facilitation cascade (Thomsen *et al.* 2010).

Bioturbation, defined as particle displacement and physicochemical sediment modifications resulting from the activity of organisms, can be understood fundamentally as a type of allogenic ecosystem engineering (Levinton 1995; Lohrer *et al.* 2004; Meysman *et al.* 2006; Mermillod-Blondin & Rosenberg 2006; Nogaro *et al.* 2009; Kristensen *et al.* 2012; Meadows *et al.* 2012; Chakraborty *et al.* 2022). In its broader sense, bioturbation also includes biogenically induced water movement, a process otherwise referred to as bioirrigation (Kristensen

et al. 2012). Bioirrigation can be subdivided into active and passive (Meile *et al.* 2001). Active bioirrigation involves burrow ventilation that takes place when animals purposely flush their open-ended (i.e. two or more openings at the surface) or blind-ended (i.e. one opening at the surface) burrows with bottom waters (Kristensen *et al.* 2012). Passive bioirrigation takes place when a burrow is oriented in relation to dominant currents and burrow architecture itself promotes fluid circulation facilitating eddy formation (e.g. the impact of the tunnel and heart-shaped chambers on flow velocity in the ichnogenus *Halimedides*; Gaillard & Olivero 2009). This type of bioirrigation also increases endobenthic oxygenation (Meile *et al.* 2001). Bioirrigation triggers transport of solutes both from the water column to the burrow and out of the burrows to the overlying water. It is important to consider that sediment reworking and bioirrigation may occur at the same time (Kristensen *et al.* 2012).

Ichnology, the study of animal–substrate interactions, has a long research history of assessing bioturbation, as well as the related processes of bioerosion (biological penetration and corrosion of hard substrates) and biodeposition (production or concentration of sediment by the activities of an organism) (Neumann 1966; Frey & Wheatcroft 1989; Bromley 1992). The focus of ichnology is not only the processes involved in bioerosion and bioturbation, but also the final products: non-discrete (i.e. biodeformational structures) or discrete biogenic structures (i.e. trace fossils or ichnofossils). Trace fossils preserve distinct morphological features (e.g. burrow architecture, wall, infill) that allow inferences on the function of the structures (Bromley 1990; Buatois & Mángano 2011a). Non-discrete, biodeformational structures can create a mottled texture and provide significant information on animal–sediment interactions. Both components, discrete and non-discrete structures, are considered part of ichnofabrics, which refers to any aspect of the texture and internal structure of a substrate due to bioturbation and bioerosion (Bromley & Ekdale 1986; Droser & Bottjer 1993).

Trace fossils hold an immense potential to explore the deep past from the perspective of macroevolution and evolutionary palaeoecology. They provide evidence of the activity of soft-bodied animals, have a continuous record through key times in the history of the biosphere, and display a close link with behaviour, environmental factors and ecosystem engineering (Mángano & Buatois 2020). On the negative side, there are some limitations, including an uncertain affiliation to a producer in many instances (particularly regarding the wide array of potential worm-like tracemakers), the role of taphonomic constraints (e.g. erosion of the mixed layer), and the impossibility of measuring some numerical variables (e.g. biodiffusion coefficient) in modern ecosystems.

The fact that trace fossils have received less attention and are not frequently considered as a source of information in evolution, compared with their potential in sedimentary geology, merits some further discussion. It may be argued that the success of ichnology in facies analysis and palaeoenvironmental reconstructions has emphasized an adaptationist and externalist research program that views trace fossil assemblages (regardless of their ichnotaxonomic composition) as behavioural units that record the functional response of animals to the environment. From this perspective, recurrent ichnocoenoses (i.e. assemblages that record the work of a community) are essentially shaped/modelled by environmental controls (Buatois & Mángano 2011a; Mángano 2021). This has negatively impacted viewing bioturbation as a form of ecosystem engineering since it resulted in an underappreciation of the pro-active role of organisms in their interaction with the substrate. However, this situation started to change roughly twenty years ago, and this trend has accelerated very recently (e.g. Mángano *et al.* 2002; Marenco & Bottjer 2007; Mángano & Buatois 2014, 2020; Minter *et al.* 2016, 2017; Herringshaw *et al.* 2017; Zhang *et al.* 2017; Cribb *et al.* 2019, 2023; Buatois *et al.* 2020; Cribb & Bottjer 2020; Darroch *et al.* 2021; Feng *et al.* 2022; Laing *et al.* 2022; Kolesnikov *et al.* 2023).

In the modern world, the role of bioturbators as ecosystem engineers is apparent across a wide spectrum of spatial scales, from that of an individual burrow (e.g. Aller 1980) to that of the whole globe (e.g. Bianchi *et al.* 2021). Physical and chemical effects that result from bioturbation and bioirrigation that modify the availability of resources are apparent at the individual burrow scale. Physical effects include changes in substrate consolidation by either increasing water content or increasing firmness, modifying grain size by binding grains into pellets, and introducing mucus as a burrow lining (Bromley 1996). These changes in substrate properties affect the composition of the endobenthos, promoting colonization by some animals but excluding others. Chemical effects are represented by a variety of reactions that take place during both construction of permanent burrows and formation of more transient biogenic structures. In this scenario, bioturbation impacts on biogeochemical reactions by affecting the availability of resources, such as carbon and nutrients, and modifying abiotic conditions, such as redox and temperature (Kristensen *et al.* 2012). These changes result in increased or decreased microbial reaction rates that can impact negatively or positively on different bacterial consortia, meiofauna and macrofauna (e.g. Aller 1994; Gutiérrez & Jones 2006; Volkenborn *et al.* 2007; Bartoli *et al.* 2020; Cariou *et al.* 2021). These effects can be traced to the scales of a whole community (synecology of bioturbation *sensu* Bromley 1996), geographic regions, or the global ocean and coastal waters.

However, upscaling is challenging due to several factors, including lack of seafloor data that would allow the complexity of benthic spatial variability to be captured (Bianchi *et al.* 2021). At the large end of the spatial spectrum, climate change may trigger variations in the distribution and abundance of benthic organisms and in the rate of sediment mixing and bioirrigation in platform areas (Bianchi *et al.* 2021). Temporal scales are particularly relevant when contrasting shallow (i.e. from the coastline to the shelf break) and deep (beyond the slope break) waters since most active carbon cycling with the macrobiota takes place in the former over the short term, but the latter is relevant as well over the long term (Bianchi *et al.* 2021).

From an applied perspective, human impact on bioturbation is becoming a topic of utmost importance due to the severity of current environmental challenges. This is particularly imperative for predicting future animal-mediated biogeochemical cycling due to climate change (Weinert *et al.* 2022). In a future scenario characterized prominently by warming, hypoxia and acidification, reduced bioturbation and bioirrigation, and shallowing of the redox discontinuity surface are some of the predicted consequences based on modern observations of marine shelves (Bianchi *et al.* 2021). Terrestrial and freshwater bioturbators play a major role in improving ecosystem health by reducing soil compaction, increasing nutrient cycling, carbon storage, microbial diversity, plant recruitment, and soil moisture, and changing redox potential; their disappearance may result in cascading effects at ecosystem scale (Beca *et al.* 2022; Chakraborty *et al.* 2022). On a positive note, experiments show that introduction of key bioturbators may help in remediation (Bugnot *et al.* 2022). In marine environments, understanding how bioturbators are directly affected by humans encompasses activities performed in the sea (e.g. trawling, mining) and those taking place on land but with consequences in the oceans (e.g. accelerating erosion and sediment delivery due to deforestation) (Widdicombe *et al.* 2004; Bianchi *et al.* 2020, 2021; de Borger *et al.* 2020; Vornsand *et al.* 2024).

Although bioturbators have a profound impact on modern ecosystems, assessing their role in terms of modification of the environment resulting in changes at community and ecosystem scales in the fossil record is not straightforward (Laing *et al.* 2022). These nuances pose the following question: How can we assess ecosystem engineering across different temporal and spatial scales? The issue of employing the appropriate tool for a specific question at a particular scale in the study of the fossil record can hardly be overemphasized (Nanglu & Cullen 2023). The goal of this paper is to offer some clues about how to approach such a complex problem. In doing so, we will explore the significance of bioturbation from the

perspective of ecosystem engineering in time and space across a wide array of scales by providing specific examples.

THE ICHNOLOGICAL TOOLKIT

To fully realize the potential of ichnology as a valuable source of information for reconstructing the history of life and the role of ecosystem engineering, a wide range of concepts, tools, and proxies operating at different scales need to be used. Some of these have been exported and adapted from palaeobiology and ecology, and new ones have been developed as well. Among these, we may mention degree of bioturbation, intersection grids, ichnodiversity, ichnodisparity, multidimensional ecospace and ecosystem engineering cubes, ecosystem engineering impact, ichnoguilds, and spindle diagrams.

Measuring the degree of bioturbation (e.g. ichnofabric index, bioturbation index, bedding-plane bioturbation index) as a proxy to infer the degree of infaunalization and surface coverage has been a popular approach in ichnological studies aimed at evolutionary palaeoecology (Reineck 1963; Droser & Bottjer 1986; Taylor & Goldring 1993; Miller & Smail 1997; Dorador & Rodríguez-Tovar 2018). If integrated with other proxies (see below) and used with proper evaluation of the sedimentological and stratigraphic context, this becomes a valuable tool. However, before making any inference with respect to bioturbation potential and ecosystem engineering, many features need to be considered. These include establishing the location of the colonization surface and differentiating between single colonization events and burrow overprinting due to the work of several communities or to the upward migration of a cohort of tracemakers in response to sedimentation through an ichnofabric analysis (Bromley & Ekdale 1986; Svrda 2014, 2016).

Bioturbation tends to be unevenly distributed on bedding planes (e.g. Mitchell *et al.* 2022). To account for such variability, the intersection grid technique has been developed (Marenco & Bottjer 2010; Marenco & Hagadorn 2019). This approach allows for statistical treatment of sedimentological and ichnological data. The intersection grid technique is useful for quantifying spatial heterogeneity and patchiness at a local extent (Marenco & Hagadorn 2019; Mángano *et al.* 2022).

To undertake a more in-depth reading of the trace-fossil record, it is important to take the actual composition of ichnofaunas into consideration. Changes in ichnodiversity through time have long been used to unravel the macroevolutionary dynamics of evolutionary radiations and colonization trends in different environments (Crimes 1974; Seilacher 1974; Orr 2001; Uchman 2004; Buatois & Mángano 2018). Construction of

ichnodiversity curves requires critical ichnotaxonomical re-evaluation to avoid using inconsistent schemes. Ichnodiversity is the number of ichnotaxa present at a certain ichnotaxonomical rank and, accordingly, is more a measurement of taxon richness than of morphological diversity (Buatois & Mángano 2013). More recently, there have been attempts to quantify abundance as well, allowing evaluation of both the number of ichnotaxa and the degree of dominance (Wisshak *et al.* 2011; Knaust *et al.* 2014). A related concept, ichnodisparity, has been introduced to capture variability of morphological plans in trace fossil architectures, yielding insights into large-scale innovations in body plan, locomotory system and/or behavioural strategy (Buatois & Mángano 2013; Buatois *et al.* 2017). Hence, ichnodisparity aims to reflect large-scale innovations that are more fundamental than those captured by ichnodiversity. To assess ichnodisparity, categories of architectural design have been defined (Buatois *et al.* 2017).

Emphasis on assessing ichnodiversity and ichnodisparity trajectories should not be done at the expense of overlooking what each of the ichnotaxa means in terms of its mode of life and style of ecosystem engineering. This can be done using two sets of cubes. One set evaluates modes of life (Bambach *et al.* 2007) and comprises three axes corresponding to tiering, motility and feeding mode, whereas the other set deals with styles of ecosystem engineering (Buatois *et al.* 2020) and focuses on tiering, mode of sediment modification, and mode of sediment interaction. This approach, known as multidimensional ecospace and ecosystem engineering analysis, was introduced less than a decade ago in ichnology (Minter *et al.* 2016, 2017) and is gaining acceptance as a way of summarizing and analysing the trace-fossil record in a systematic fashion from the perspective of ecospace utilization and ecosystem engineering (e.g. Cribb *et al.* 2019, 2023; Cribb & Bottjer 2020; Buatois *et al.* 2020; Darroch *et al.* 2021; Feng *et al.* 2022; Kolesnikov *et al.* 2023). The multidimensional ecospace and ecosystem engineering analysis results from the articulation through the lens of ichnology of two different research traditions: ecospace utilization from palaeobiology (Bambach 1983; Bambach *et al.* 2007; Bush *et al.* 2007), and functional groups from marine benthic ecology (François *et al.* 2002; Solan & Wigham 2005; Michaud *et al.* 2005, 2006; Kristensen *et al.* 2012).

In this approach, mode of sediment interactions is based on a scheme by Bromley (1996), which comprises intrusion, compression, excavation, and backfilling. Intrusion refers to sediment displacement as the animal moves through, but the sediment closes behind it. The sediment is mixed by eddy diffusion. Different types of polychaetes and naticid gastropods use intrusion. Compression corresponds to sediment movement and compaction around the animal as it passes through. Amphibaenids, a group

of limless vertebrates, as well as some polychaetes and bivalves, use compression to penetrate the sediment (Bromley 1996). Excavation reflects active loosening and bulk transport of sediment from one spot to another. Crustaceans and fish, as well as mammals, are typical excavators (Bromley 1996). Backfilling records active backward sediment movement around or through the animal. This mode of sediment interaction is epitomized by spatangoid echinoids.

Mode of sediment modification deals with the way the organisms impact on and rework sediment based on standardized categories adapted from marine benthic ecology (François *et al.* 1997, 2002; Solan & Wigham 2005). The categories employed for the analysis of the trace-fossil record are biodiffusers, gallery biodiffusers, conveyors and regenerators (Minter *et al.* 2017; Buatois *et al.* 2020). Biodiffusers move sediment particles over short distances, in a similar fashion to molecular or eddy diffusion, and may occur in different tiers. Examples are represented by the spatangoid *Echinocardium* (Lohrer *et al.* 2004, 2005) and the brittle star *Amphiura filiformis* (Gilbert *et al.* 2007). Gallery biodiffusers generate rapid redistribution of sediment particles from one point in the sediment profile to another, resulting in diffusive local biomixing of particles typically due to the construction of dwelling burrows. The polychaete *Nereis diversicolor* is a typical example (François *et al.* 2002). Conveyors are oriented vertically and actively transport sediment particles at a non-local scale, across and within different tiers in the sediment, reaching zones that are beyond the reach of biodiffusers. Both upward and downward conveyors are included in this category as it is not always possible to differentiate between the two in the fossil record. In the modern world, the lugworm *Arenicola marina* is an upward conveyor, whereas the polychaete *Cirriformia grandis* is a downward conveyor (Kristensen *et al.* 2012). Regenerators construct actively maintained burrows and, in doing so, they constantly move sediment from within the sediment to the surface. Sediment transported to the surface may then be reworked by currents and waves. Examples of this category are the ghost crab *Ocypode* and the fiddler crab *Uca* (Kristensen *et al.* 2012).

A method for quantifying ecosystem engineering impact was proposed shortly after the ecospace occupation and ecosystem engineering cubes (Herringshaw *et al.* 2017). This is a metric in which ichnotaxa are scored as the sum of their tier, functional group, and likelihood of bioirrigation; the greater the score, the greater the ecosystem engineering impact of a particular ichnotaxon. Herringshaw *et al.* (2017) suggested that a range of values could be possible across these criteria for any given ichnotaxon. There are some limitations, however, to the methodological basis of this measure as the values assigned to certain criteria are conflation

(Mángano & Buatois 2020; Laing *et al.* 2022). Nevertheless, it can help with identification of which ichnotaxa are likely to be having relatively greater impacts on sediments and it is a useful tool for analyses at the short- to intermediate-term temporal scale and local spatial scale to characterize changes in ecosystem engineering through a sedimentary succession. In addition, further power could lie in incorporating the abundances and sizes of each ichnotaxon when studying measured stratigraphic sections as density and size have proved to be significant variables in modern ecological studies (Moore 2006; D'Andrea & DeWitt 2009; Raynaud *et al.* 2013; Albertson & Daniels 2018; Licci *et al.* 2019; Johnson-Bice *et al.* 2022). This approach has been applied when analysing ecosystem engineering impact of whole trace fossil assemblages, by summing across the ichnotaxa present at the short-term temporal and local spatial scales (Kolesnikov *et al.* 2023; Marusin & Bykova 2023; Liu *et al.* 2024), the intermediate-term temporal and local spatial scales (Cribb *et al.* 2019) and the intermediate-term temporal and global spatial scales (Cribb & Bottjer 2020) (see next section for definitions of spatial and temporal scales).

Another useful concept, which has been adapted from biology and palaeobiology, is that of the ichnoguild (Bromley 1990, 1996). An ichnoguild consists of three parameters: (1) bauplan; (2) food source; and (3) use of space. The concept of the ichnoguild is essential to unravelling the adaptive strategies of benthic organisms and evaluating niche partitioning within the substrate. Although this concept remains underutilized so far, the number of studies that employ it for the analysis of ichnofaunas of different environments and ages is gradually growing (e.g. Ekdale & Bromley 1991; Bromley 1994; Buatois *et al.* 1998, 2014, 2022a; Mángano *et al.* 2002; Buatois & Mángano 2003; Baldwin *et al.* 2004; Mángano & Buatois 2004; Desai *et al.* 2008; Tapanila 2008; Laing *et al.* 2019; Olivero & López-Cabrera 2023).

Finally, spindle diagrams have recently been used to plot changes in ichnodiversity at ichnospecific rank (Zhang *et al.* 2022). These diagrams allow a distinction between bottom-heavy and top-heavy ichnogenera, corresponding to those ichnogenera that display an increase in the number of ichnospecies earlier or later in the Phanerozoic, respectively. In turn, timing of diversification at ichnospecies rank is linked with evolutionary radiations and the ichnological equivalents of the Cambrian, Palaeozoic and Modern evolutionary faunas.

Not all these concepts and tools have been applied from a macroevolutionary perspective to the same extent and accuracy. Furthermore, only the multidimensional ecospace and ecosystem engineering analysis, and ecosystem engineering impact have been specifically designed with the goal of evaluating ecosystem engineering. However, all these approaches have the potential to provide

insights in this regard. Therefore, whenever possible, all these should be used in an integrated fashion to offer a more accurate and holistic reading of the trace-fossil record from a perspective of ecosystem engineering across spatial and temporal scales.

UNRAVELLING THE IMPACT OF ECOSYSTEM ENGINEERING ACROSS SPATIAL AND TEMPORAL SCALES

We have selected some examples from the fossil record to demonstrate how ichnological data can be treated from the perspective of ecosystem engineering at different scales of analyses making use of the ichnological toolkit, starting from the small scale, and moving into large-scale patterns both in space and time. To frame this section, we have constructed a matrix in which we locate these examples in terms of three categories of spatial (i.e. local, regional, and global) and temporal (i.e. short-term, intermediate, and long-term) scales (Fig. 1). In terms of temporal scale, we define: (1) short-term temporal scale as encompassing from the snapshot of a point in time at a particular stratigraphic level to the time involved in the deposition of bedsets or coeval horizons; (2) intermediate-term temporal scale as within a geological period or across a boundary between geological periods; and (3) long-term temporal scale as spanning several geological periods, and can extend to whole geological eras or the whole Phanerozoic. In terms of spatial scale, we define: (1) local spatial scale as data from a single locality or stratigraphic succession; (2) regional spatial scale as data from a single region/basin to several palaeocontinents/basins and latitudinal belts; and (3) global spatial scale as worldwide data.

Adopting a specific scale dictates the types of observations to be made, approaches to be adopted, and explanatory driving processes/mechanisms to be proposed. In the case of short-term and local scales, observations are made *in situ* at specific localities on discrete beds to bedsets. For short-term and regional scales, the data are gathered at several locales along strike or dip involving individual basins. At intermediate-term and local scales, observations are made *in situ* at specific localities spanning from parasequences and parasequence sets to sequences. In the cases of intermediate-term and regional scales, the data are compiled either within an individual basin or encompassing multiple basins and the stratal stacking pattern analyses typically range from parasequences and parasequence sets to sequences. In the cases of intermediate-term and global spatial scale, long-term and regional scale, and long-term and global scales, the data may be secondarily obtained from diverse sources such as trace fossil assemblages published in the literature or available

		SPATIAL SCALE		
		LOCAL	REGIONAL	GLOBAL
TEMPORAL SCALE	SHORT-TERM	<ul style="list-style-type: none"> • Three-dimensional burrows in Cambrian carbonates • Burgess Shale-type carapaces • Jurassic arenicoloid mounds • Bioturbation in a Pennsylvanian equatorial tidal flat 	<ul style="list-style-type: none"> • Bioturbation trends along a Miocene tropical clastic belt 	<p>Theoretically possible but prevented due to lack of worldwide chronostratigraphic surfaces</p>
	INTERMEDIATE	<ul style="list-style-type: none"> • Onset of ecosystem engineering styles in the Ediacaran–Cambrian Chapel Island Formation • Bioturbators as ecosystem engineers in the Ediacaran–Cambrian Nama Group • Bioturbators as ecosystem engineers in the Cambrian Nokhtuisk Formation 	<ul style="list-style-type: none"> • Cambrian bioturbation in the Great Basin of western United States • Ecosystem engineering during the end-Permian mass extinction in China • Impact of bioturbation in an Ordovician equatorial carbonate belt • Palaeogeographic patterns in Ordovician colonization of the deep sea 	<ul style="list-style-type: none"> • Bioturbators as ecosystem engineers in the Cambrian Explosion • Bioturbators as ecosystem engineers in the Ordovician Radiation • Bioturbation and the end-Permian mass extinction
	LONG-TERM	<p>Theoretically possible but prevented due to lack of continuous successions through the whole Phanerozoic in a single spot</p>	<ul style="list-style-type: none"> • Ecosystem engineering in high-latitude environments through geologic time 	<ul style="list-style-type: none"> • Palaeozoic invasion of the land • Styles of ecosystem engineering in marine environments through the Phanerozoic

FIG. 1. Combination matrix for spatial and temporal scales highlighting examples discussed in this paper. Combinations with a red background are not applicable to the fossil record.

databases that are used in metanalysis, or it may be compilations of primary data obtained from multiple measured stratigraphic sections. In terms of approaches, ideally, all elements of the ichnological toolkit may be used regardless of the scale. However, some elements of the toolkit are more appropriate depending on the data available. For instance, bioturbation indices and intersection grids can only be used when primary field data are available, whereas ichnodiversity, ichnodisparity and multidimensional cubes can be constructed when secondary presence/absence data is available. In contrast, explanatory driving mechanisms are scale-dependent, such as environmental conditions at the smaller scale or evolutionary radiations and the large scale, and extrapolation from one spatial or temporal scale to the other should be done with extreme care.

Not all combinations of spatial and temporal scales are applicable to the fossil record, which is particularly evident for those between contrasting end members of the scales (i.e. short term at global extent and long term at a local extent). The underlying rationale lies in the nature of the stratigraphic record. For example, a snapshot view (i.e. short-term temporal scale) at a global spatial extent, although theoretically possible, is in practice impossible due to the lack of worldwide chronostratigraphic surfaces recording global timelines, a point made repeatedly by sequence stratigraphers (Catuneanu 2022). In the same vein, long-term temporal studies performed at a local spatial scale are possible in theory but precluded by the lack of continuous successions spanning very long periods

of time at a single spot even in the locations with the most complete stratigraphic records (Fig. 1).

Short-term temporal and local spatial scales

Trace fossil information can be approached from this combination of scales, which is the one typically used by modern benthic ecologists, as most ecological studies are performed at a local extent and over short time spans (e.g. Lohrer *et al.* 2015). Although to some degree this requires a given set of conditions, the recent indication that true substrates (i.e. preserved surfaces that record the sediment–water or sediment–air interface at the time of deposition) are more common than previously envisaged (Davies & Shillito 2018, 2021) favours viewing the trace-fossil record from the perspective of snapshots in some instances. Studies at this scale can be done either from an autoecological (i.e. ecosystem engineering impact of one type of bioturbator) or syn-ecological (i.e. ecosystem engineering impact of the community) perspective. In this section, we discuss four examples of the first category (i.e. bioturbation by Mesozoic terebellid polychaetes as a trigger of microbial activity; the importance of three-dimensional Cambrian galleries; microbial gardens associated with Burgess Shale carapaces facilitating burrowing activities; and the work of burrowing arenicolids in a Jurassic coast), and one example of the second category (bioturbation in Pennsylvanian tidal flats).

Bioturbation by Mesozoic terebellid polychaetes as a trigger of microbial activity

Studies of modern bioturbation have provided extensive evidence of the role of bioturbation in microbial enrichment. For example, using their tentacles, terebellid polychaetes produce mucus that adheres to the surrounding sediment particles (Grémare 1988). As is the case for different worms, mucus produced by terebellid polychaetes may attract microbial activity (Aller & Aller 1986). Mucus promotes metal adsorption and mineral nucleation reactions on burrow linings, generating nutrients used by their symbiotic microbial colonies (Lalonde *et al.* 2010). Other types of polychaete construct tubes which have agglutinated peloids formed by bacterial sulfate reduction (Guido *et al.* 2014).

Although similar studies in the fossil record are rather sparse, this may reflect more the lack of the right tools for this scale of analysis rather than a real absence of this type of interaction. Zorn *et al.* (2007) analysed the isotopic composition of authigenic siderite and calcite cements in the burrow *Rosselia socialis* from the Upper Cretaceous of Alberta, Canada. These authors found that the mucus lining acted as a carbon source for an anaerobic microbial community hosted in the burrow wall. In the same fashion, Kołodziej *et al.* (2024) studied the burrow *Macroterebella hoffmanni* from the Upper Jurassic to the Lower Cretaceous of Romania, also attributed to terebellid polychaetes, concluding that the formation of the micropeloidal texture of the burrow wall was due to bacterially mediated precipitation. Other studies in the fossil record have proposed microbial enrichment for other types of burrow typically associated with pellet formation (e.g. García-Ramos *et al.* 2014; Izumi *et al.* 2015), therefore underscoring the potential of this line of research.

Three-dimensional burrows in Cambrian carbonates

Carbonate ichnology lags siliciclastic ichnology in the number of studies and available models (Buatois & Mángano 2011a). However, there is recent awareness of the important role of bioturbation in Cambrian carbonate platforms in North China. Zhang *et al.* (2017) documented deep-tier (up to 32.4 cm) burrow mazes in lower Cambrian nearshore carbonates of Henan Province. In these deposits, a high density of three-dimensional galleries was conducive to significant disruption of the sedimentary fabric. These authors employed ImageJ analysis to calculate spacing among burrows and analyse burrow fills and walls through the study of thin sections. In many places, burrow segments are within 5 mm of each other, which allowed their oxygenated zones to meet, facilitating organic carbon and dissolved inorganic nitrogen fluxes in

an otherwise impermeable sediment matrix. In addition, these authors argued that excavation of these galleries may have increased ammonium fluxes across the sediment–water interface and regeneration of nutrients. Another potential effect was the deepening of the redox discontinuity surface with the consequent expansion of aerobic bacteria. Similar types of gallery have been analysed from a similar perspective in subsequent studies dealing with overlying units in this same area, including carbonates of both early (Fan *et al.* 2021) and middle (Wang *et al.* 2019; Liu *et al.* 2024) Cambrian age. These studies underscore the environmental impact of deep-tier, extensive bioturbation in Cambrian carbonate platforms.

Trace fossils associated with Burgess Shale-type carapaces

One of the ichnological signatures of Burgess Shale-type biotas is the association of trace fossils and carapaces (e.g. Mikuláš 2000; Zhang *et al.* 2007; Lin *et al.* 2010; Peel 2010; Mángano 2011; Mángano *et al.* 2012, 2019; Mikuláš *et al.* 2012; Schroeder *et al.* 2018). A particularly impressive case is that of nonbiomineralized carapaces of *Arthroaspis* from the lower Cambrian Sirius Passet lagerstätte of Greenland, which display delicately preserved trace fossils with a wide size range, diverse morphologies, and distinct architectures (Mángano *et al.* 2012). Although coincidental association cannot be ruled out in the case of many isolated trace fossil occurrences in contact with carapaces, systematic mapping of trails and shallow burrows suggests deliberate activity around carapaces (including both exuvia and carcasses). In other words, a palaeoecological scenario involving the use of a geochemical gradient (enhanced by the presence of the chitinous carapace) by organisms living below, but also the exploitation of enriched bacterial films above and in the immediate surrounding of carapaces, is favoured (Figs 2, 3). The fact that many structures indicate revisitation suggests that the effects of the burrowing infauna on microbial populations and geochemical conditions may have been significant. These trace fossils not only reveal grazing on surfaces engineered by *Arthroaspis* carapaces, but the trace-fossil producers also engineered the sediment properties themselves and contributed to increasing the heterogeneity of Cambrian sea floors, a perspective highlighted by the Cambrian information revolution (Plotnick 2007; Plotnick *et al.* 2010; Hsieh *et al.* 2022). It is not only the presence of the carapaces, but also the bioturbation structures themselves that are providing additional surfaces, through the presence of burrow boundaries and pellets, for bacterial growth. Most importantly, it is only through the presence of delicate trace fossils that we can detect the physical and chemical modification of the environment due to the carapace sealing

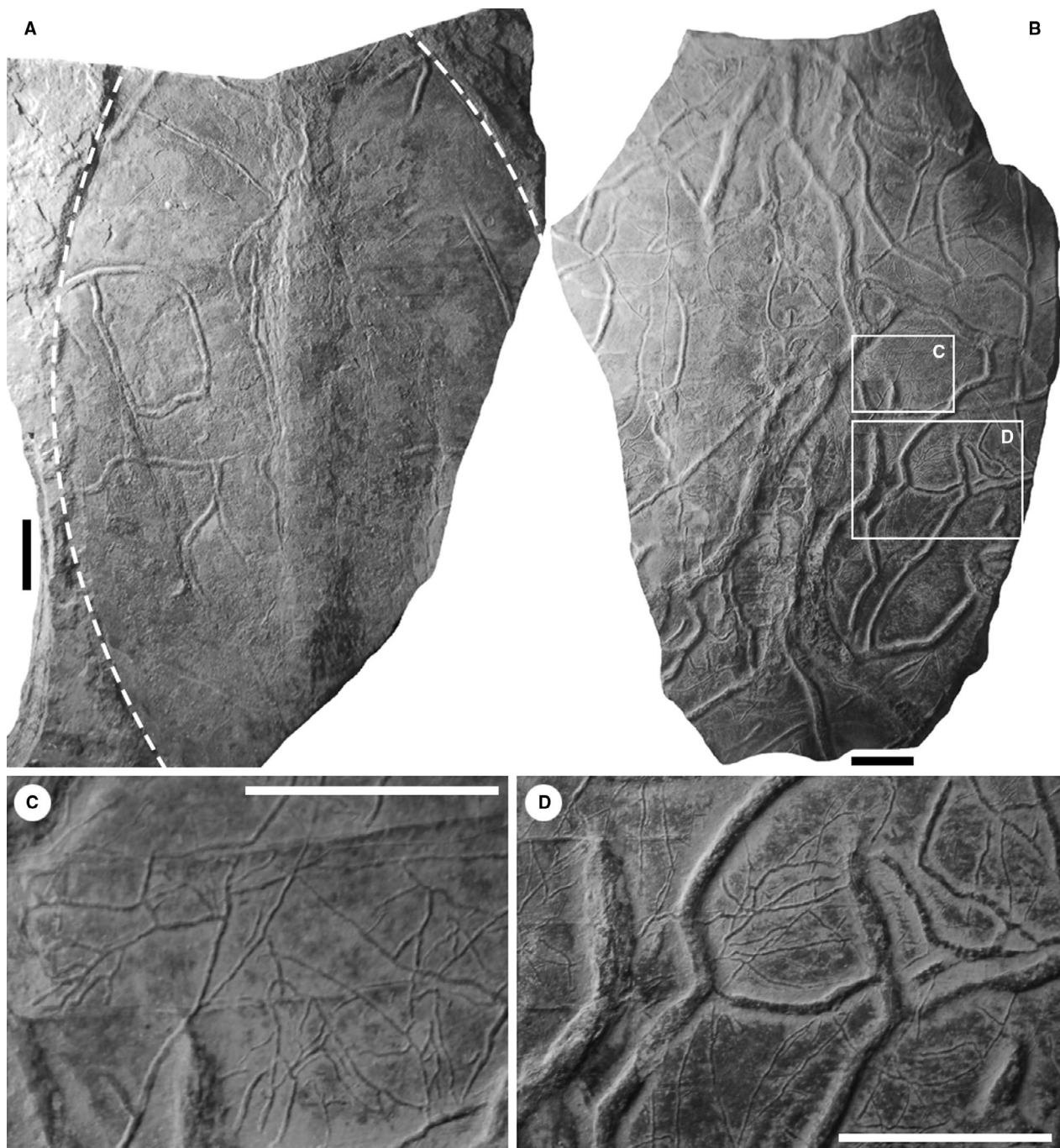


FIG. 2. Trace fossils associated with nonbiomineralized carapaces of the trilobitormorph *Arthroaspis* from the lower Cambrian Sirius Passet lagerstätte of Greenland. A, general view of *Arthroaspis* showing irregular burrow networks; sharp kink in upper right is evidence of the producer reaching carcass edge and then retracting; specimen MGUH 29706 curated by the Natural History Museum of Denmark, Copenhagen, Denmark. B, general view of *Arthroaspis* hosting irregular polygonal networks that show both true and secondary successive branching; specimen MGUH 29705. C, close-up showing delicate filament-like structures with dendritic morphology. D, close-up showing annulated burrows and filament-like structures. All scale bars represent 1 cm.

the sediment. In modern marine settings, a similar role in the modulation of resources (albeit involving different organisms and trophic types and at a much larger scale)

is played by sunken whale carcasses, which deliver organic material to the sea bottom, creating real oases in a food-depleted environment (e.g. Smith & Baco 2003; Goffredi

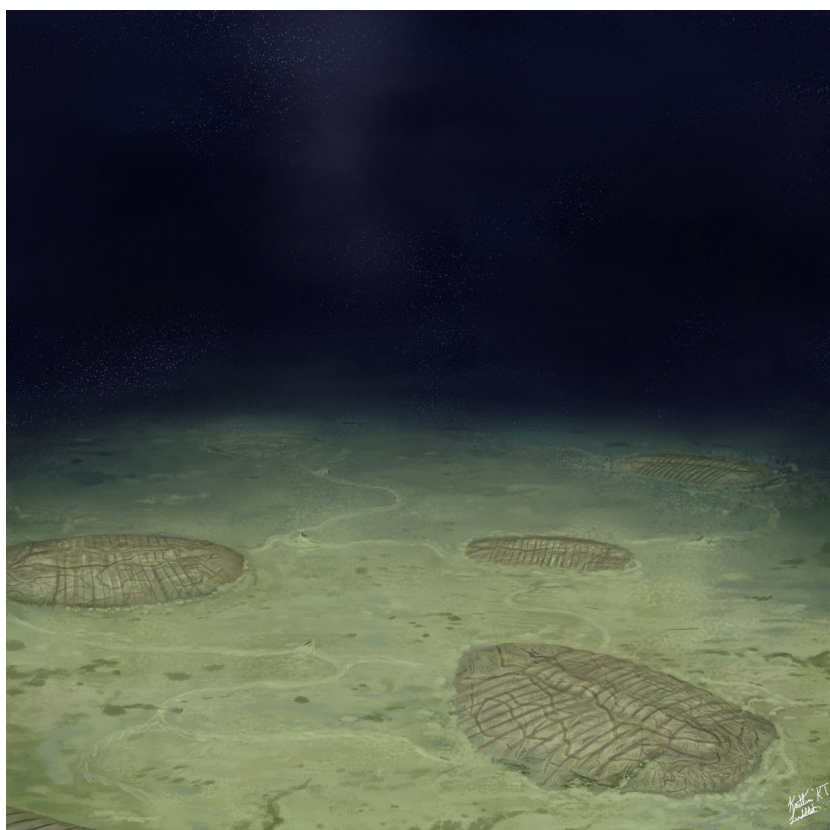


FIG. 3. Idealized reconstruction of Sirius Passet seascapes with *Arthroaspis* promoting spatial heterogeneity. Illustration by Kaitlin Lindblad.

et al. 2004; Higgs *et al.* 2014; Onishi *et al.* 2020). The impact of whale falls has been underscored by the recognition of these organisms as ecosystem engineers (Roman *et al.* 2014).

Arenicolid burrows in a Jurassic coast

Modern tidal flats are important research grounds for modern benthic ecologists. *Arenicola marina* and related species have been identified as powerful ecosystem engineers in these environments (e.g. Rijken 1979; Reise *et al.* 2001; Volkenborn *et al.* 2007, 2009; Woodin & Wethey 2009; Woodin *et al.* 2010; Wendelboe *et al.* 2013). The discovery of exceptional rippled palaeosurfaces in Upper Jurassic coastal deposits of Spain that preserve faecal casting mounds identical to those of modern arenicolids allows the work of these animals (Fig. 4), with a meagre body-fossil record, to be tracked back in time (Mángano *et al.* 2024). Notably, these trace fossils display similar densities to those of modern arenicolid populations, allowing solid comparisons in terms of ecosystem engineering impact, including inferences for quantifying sediment reworking and bioirrigation potential

(Cadée 1976; Riisgård *et al.* 1996; Mángano *et al.* 2024). As is the case of modern counterparts, it is expected that arenicolids in the past have substantially affected their environment through the generation of seabed topography and by impacting the benthos, as well as sediment characteristics and biogeochemistry. The presence of grazing trails in these mounded surfaces is regarded as evidence of fertilization and modulation of food resources for other species (Mángano *et al.* 2024).

Bioturbation in a Pennsylvanian equatorial tidal flat

Ancient tidal flats also can be analysed by evaluating the impact of a whole suite of bioturbators. The Waverly trace fossil site of eastern Kansas is host to an extremely diverse and abundant ichnofauna that records animal–substrate interactions in a late Pennsylvanian equatorial tidal flat (Mángano *et al.* 2002). These deposits display a marked spatial heterogeneity in trace fossil distribution that is appreciable at both the larger scale of zonal distribution along the entire tidal range and at the small scale of spatial segregation within specific zones of the tidal flat (Mángano *et al.* 2002). The latter may reflect

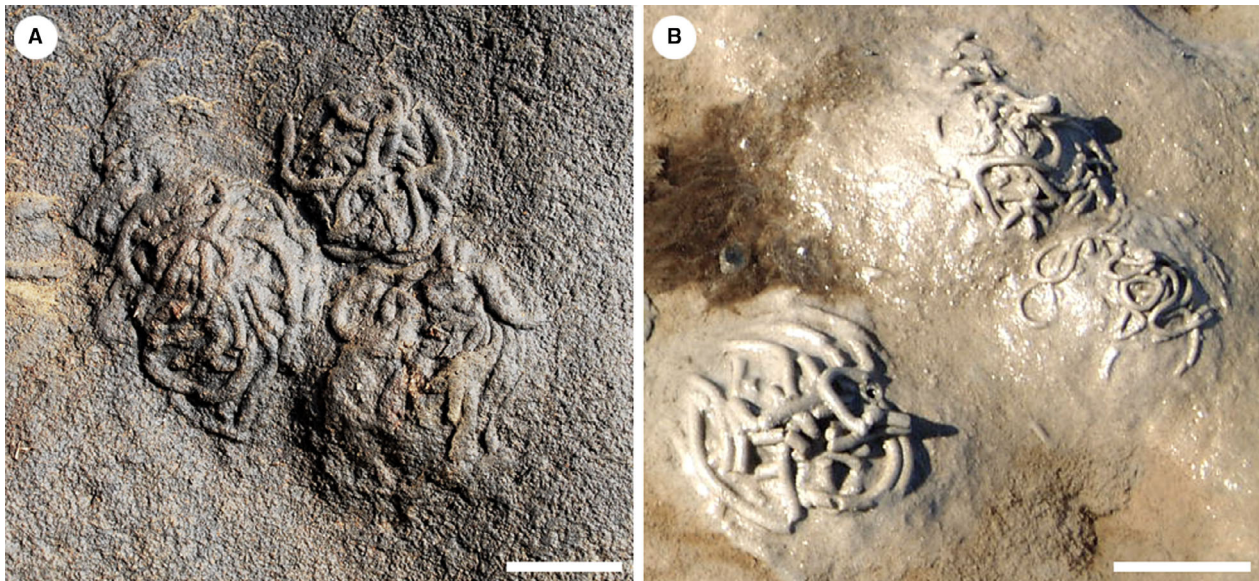


FIG. 4. Faecal casts by arenicolid polychaetes. A, ancient example from the Upper Jurassic Lastres Formation of Asturias, northern Spain; specimens MUJA-3826-10, 11, and 12 curated by the Museo del Jurásico de Asturias, Colunga, Spain. B, modern example from the Wadden Sea tidal flats, northern Germany. Both scale bars represent 1 cm.

the formation of distinct microhabitats (e.g. sediment mounds and ponded areas) and partitioning of energy resources (e.g. food concentrated in ripple troughs). Specifically, bioturbators impacted substrate stability in various ways in the different patches that resulted from spatial heterogeneity. The mucus-lined, U-shaped burrow *Protovirgularia bidirectionalis* may have reduced resuspension and erosion, therefore representing the record of a sediment stabilizer. A similar role is apparent for lined vertical domiciles, most likely produced by worms. This interpretation is further supported by the preferential concentration of both types of burrows in small mounds within the palaeosurface (Mángano *et al.* 2002). Through trapping of tidally transported particles, these organisms created a distinctive microtopography on the sediment surface. In contrast, detritus and deposit feeders are regarded as sediment destabilizers. Examples at Waverly include high density suites of different ichnospecies of the worm trace fossil *Nereites*, most notably *N. missouriensis*, which are thought to have encapsulated within the sediment large quantities of defecation products. Sediment destabilizing is also illustrated in these deposits by *Curvolithus simplex*, which is attributed to predatory flatworms or gastropods, whose intruding up-and-down movements were most likely detrimental for substrate stability. The general patchiness in the spatial distribution of biogenic structures in this ancient tidal flat and the scarcity of permanent domiciles of suspension feeders in deposits densely burrowed by sediment destabilizers support trophic group amensalism (*sensu* Rhoads & Young 1970).

Overall, the emerging picture from the Waverly locality is one of a complex Pennsylvanian tidal flat ecosystem characterized by spatial heterogeneity in which different styles of bioturbation impacted substrate stability and modulation of food resources, actively affecting the distribution of the intertidal benthos.

Short-term temporal and regional spatial scale

Evaluating short-term changes at regional extent is challenging as it requires high-resolution correlations. However, an understanding of sequence stratigraphic architecture may aid in providing the temporal framework to reconstruct styles of ecosystem engineering along the marine depositional profile or along strike. There is a growing number of ichnological studies that have tackled this level of stratigraphic resolution, although these are typically not focused on ecosystem engineering but on the applications of trace fossils in facies analysis and sequence stratigraphy. Most of these case studies were performed in connection with hydrocarbon exploration and reservoir characterization. The available information, however, can be read from an ecosystem engineering perspective.

Bioturbation trends along a Miocene tropical clastic belt

One of these studies is based on the subsurface analysis of shallow marine to deltaic systems along 65 km of

palaeocoastline in the Miocene of Venezuela (Buatois *et al.* 2012). These authors demonstrated significant along-strike changes in trace fossil assemblages, with deposits formed under fully marine conditions (particularly those formed on the updrift side of distributary channel mouths) being intensely bioturbated and dominated by *Scolicia*, a trace fossil produced by spatangoid echinoderms (Smith & Crimes 1983; Plaziat & Mahmoudi 1988; Uchman 1995; Uchman & Krenmayr 1995; Asgaard & Bromley 2007; Carmona *et al.* 2020; Buatois *et al.* 2023a). Notably, the disappearance of this ichnogenus in the coeval deposits formed under the direct influence of river discharge (e.g. downdrift prodelta) in both river- and wave-dominated deltas is an indication of the low tolerance to salinity fluctuations, and particularly brackish water conditions, of the producer (Buatois *et al.* 2008). Modern studies have emphasized the impact of some species of spatangoid urchins as ecosystem engineers. Burrowing by *Echinocardium*, a highly efficient bioturbator, changes nutrient fluxes and improves production by microphytobenthos (Lohrer *et al.* 2004, 2005, 2013, 2015). On the contrary, its elimination negatively impacts benthic-pelagic processes, as well as primary and secondary production (Lohrer *et al.* 2004). From this perspective, a transect along the studied Miocene palaeoshoreline helps to delineate the impact of key bioturbators that show a heterogeneous distribution along strike.

Intermediate-term temporal and local spatial scale

Combining these two disparate temporal and spatial scales can be done in the case of continuous successions in which subenvironments are vertically repeated because of high-frequency sea-level changes, typically resulting in the stacking of parasequences forming parasequence sets. Comparing similar subenvironments along local successions is essential to discriminate between environmental and evolutionary patterns (MacNaughton & Narbonne 1999; Shahkarami *et al.* 2017; Gougeon *et al.* *in press*). This approach has been undertaken to assess the ecosystem engineering impact of bioturbation across the Ediacaran–Cambrian interval in the Global Boundary Stratotype Sections and Points (GSSP) for the Cambrian System. Similar studies have been performed in other Ediacaran–Cambrian successions.

Onset of styles of ecosystem engineering at the GSSP for the Cambrian System

An extensive ichnological dataset framed within sedimentological and sequence stratigraphic information allows

evaluation of the diversity of styles of ecosystem engineering in a wide variety of shallow marine environments recorded in the Ediacaran–Cambrian Chapel Island Formation of Newfoundland, eastern Canada (Gougeon *et al.* *in press*) (Fig. 5). Application of the multidimensional ecospace and ecosystem engineering approach shows very few modes of sediment modification and interaction during the Ediacaran in all environments represented in the Chapel Island Formation, suggesting limited levels of ecosystem engineering prior to the Cambrian Explosion (Gougeon *et al.* *in press*). As in other Ediacaran deposits elsewhere, surficial to shallow-tier trace fossils were dominant. Despite the appearance of a wide variety of trace fossils, the early Fortunian was still characterized by relatively low levels of exploitation of the endobenthic ecospace and relatively limited diversity of styles of ecosystem engineering (see also Buatois *et al.* 2014; Herringshaw *et al.* 2017 and Gougeon *et al.* 2018). This situation started to change in the latest Fortunian and in Cambrian Stage 2, particularly in the offshore, which overall displays the highest number of styles of engineering of all environments recorded in the succession (Gougeon *et al.* *in press*).

Bioturbators as ecosystem engineers at other Ediacaran–Cambrian successions

Another unit that has been studied from this perspective is the Ediacaran–Cambrian Nama Group of Namibia (Buatois *et al.* 2018; Cribb *et al.* 2019; Darroch *et al.* 2021; Turk *et al.* 2022). These studies show that the terminal Ediacaran was characterized by an increase in the impact of ecosystem engineering in comparison to the older White Sea Assemblage. Information from the Nama Group supports the hypothesis that increased environmental disturbance by deposit- and detritus-feeding bulldozers at or close to the sediment–water interface may have played a central role in the demise of the Ediacara biota (Buatois *et al.* 2018; Darroch *et al.* 2021, 2023).

The Cambrian Stage 2 Nokhtuisk Formation of Siberia has recently been analysed in terms of the ecosystem engineering impact of bioturbation (Kolesnikov *et al.* 2023). This unit consists of poorly bioturbated marginal-marine carbonates and siliciclastics hosting abundant microbial mats and discs resembling the iconic Ediacaran body fossil *Aspidella* (Marusin & Bykova 2023). A few shallow-tier ichnotaxa have been recorded, representing very limited exploitation of the endobenthic ecospace. This study supports the notion that the agronomic revolution was diachronic and that marginal-marine settings lagged in terms of ecosystem engineering.

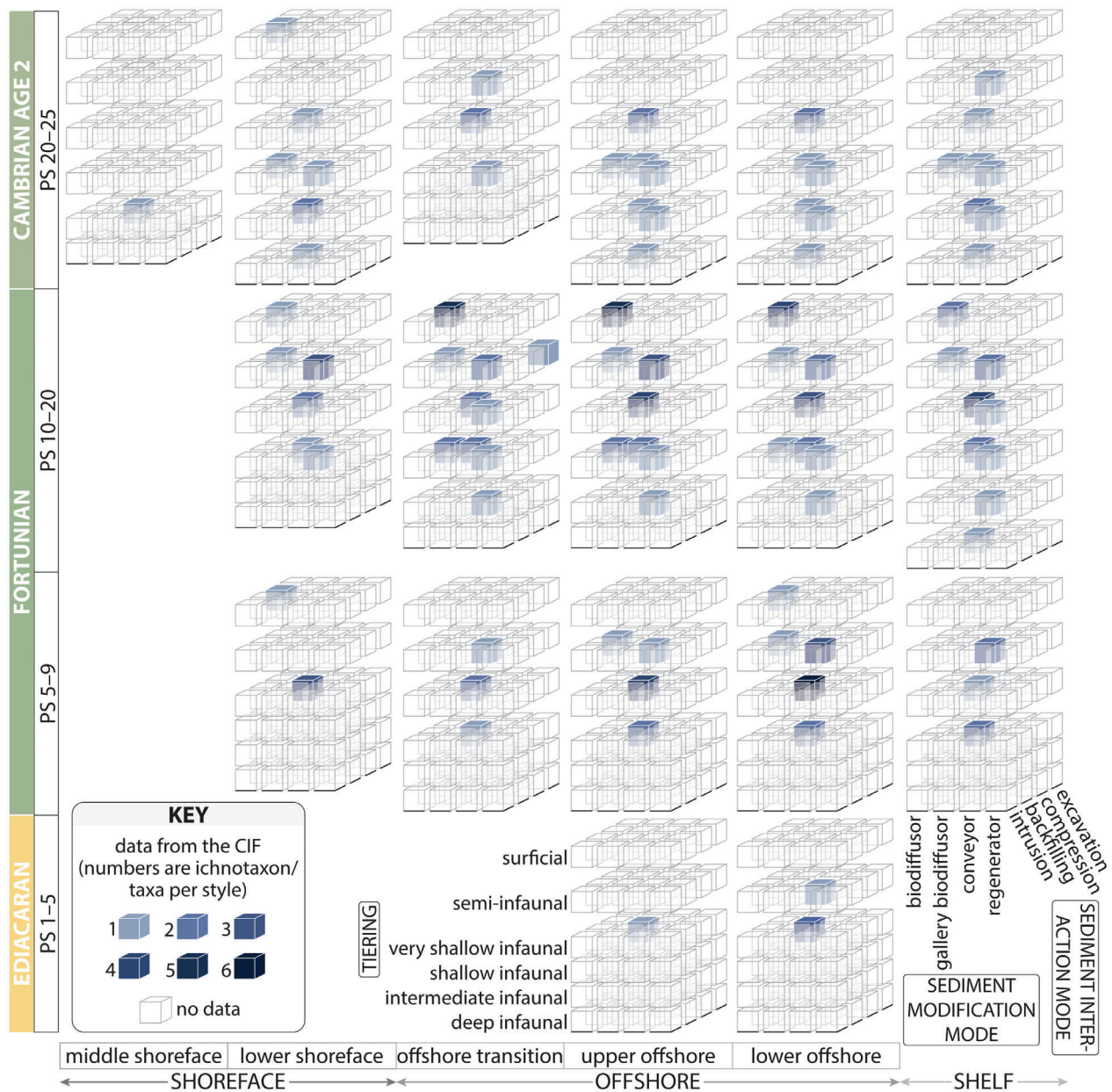


FIG. 5. Ecosystem engineering along the shallow-marine depositional profile in the Ediacaran–Cambrian boundary interval as recorded in the Chapel Island Formation (CIF) of Newfoundland, Canada. From left to right: time interval; parasequence (PS) number (delineated on higher-resolution logs, see Gougeon *et al.* in press); time–environment–ecosystem engineering matrix. The matrix shows that styles of ecosystem engineering were limited during the Ediacaran, and that they became very diverse in offshore subenvironments during the late Fortunian (PS 10–20). Absence or reduced number of styles of engineering in surficial and semi-infaunal tiers during Cambrian Age 2 are a consequence of the establishment of the sediment mixed layer (see also Gougeon *et al.* 2018).

Intermediate-term temporal and regional spatial scale

Moving from the local to the regional extent at an intermediate temporal scale encompasses studies undertaken within a single basin to those covering whole palaeocontinents (i.e. multiple basins). At the first end of the spatial spectrum, the role of bioturbation can be analysed along

the depositional profile of a specific basin to evaluate its differential impact in discrete subenvironments. Expressing these trends through a time–environment matrix allows the assessment of temporal patterns in onshore–offshore trends. In this section, we illustrate this with studies of bioturbation in the Great Basin of western United States during the Cambrian (Droser & Bottjer 1988).

Inter-basinal studies show the effects of bioturbation across wider areas, a scale of analysis that is illustrated here with the analysis of endobenthic communities across the Permian–Triassic boundary in China (Feng *et al.* 2022). Finally, plotting trace fossil information onto palaeogeographic maps allows reconstruction of the regional expression of global evolutionary events through comparisons among ancient continents and oceans. This scale of analysis allows tests of whether the impact of bioturbation at ecosystem scale may have varied from region to region. This approach is valuable to dissect if global patterns result from the addition of disparate regional trajectories. We illustrate this combination of scales with the colonization of carbonate platforms and the deep sea during the Ordovician Radiation to evaluate if there are regional patterns associated with this evolutionary breakthrough.

Cambrian bioturbation in the Great Basin of the western United States

Prior to the formalization of the concept of ecosystem engineering (Jones *et al.* 1994), Droser & Bottjer (1988) analysed bioturbation depth and bioturbation indices from inner and middle shelf settings through measured sections encompassing the whole Cambrian within the Great Basin of the USA in Nevada, Utah and California. This can therefore be viewed as an example of analysis of ecosystem engineering at the intermediate-term and regional spatial scale. Results found that bioturbation indices increased through the Cambrian, with more activity in the inner compared to the middle shelf, although maximum bioturbation depth remained relatively low and constant through this interval (Droser & Bottjer 1988). Uncertainties regarding the producers of these burrows complicate their understanding in terms of the precise style of ecosystem engineering, with gallery biodiffusers and regenerators being the most likely categories.

Ecosystem engineering during the end-Permian mass extinction in China

Analysis of endobenthic communities across the Permo-Triassic mass extinction in China (Feng *et al.* 2022) represents an additional example of the intermediate-term temporal and regional spatial scale. Ichnodiversity, ichnodisparity, ecospace occupation, and ecosystem engineering were analysed across 26 sections from the Changhsingian to the Spathian and from lacustrine, brackish, carbonate platform, carbonate ramp, lower shoreface, and shelf-slope basin settings. Results demonstrate differences

across environments, but the metrics all declined into the Griesbachian and then recovered by the Smithian in the marine realm but not until the Spathian in lacustrine environments. The decline in metrics appears to be coincident with higher temperatures and anoxia, whereas their increase corresponds with cooling and reduced anoxia (Feng *et al.* 2022). Some styles of ecosystem engineering persisted but there were generally few ichnotaxa and architectural designs in the aftermath of the extinction, and the activities of bulldozing motile deposit feeders may have inhibited the recovery of non- and facultatively motile suspension feeders (Feng *et al.* 2022).

Impact of bioturbation in an Ordovician equatorial carbonate belt

An ichnofabric characterized by deep-tier three-dimensional branching galleries is widespread in Ordovician platform carbonates forming a belt spreading from Laurentia to Baltica and Tuva that covered approximately a third of the Equator (Sheehan & Schiefelbein 1984; Kulkov 1991; Ekdale & Bromley 2003; Jin *et al.* 2012; Knaust & Dronov 2013; Zheng *et al.* 2018). These palaeocontinents were surrounded by carbonate platforms forming the shallow-water portion of the Iapetus Ocean. Although this ichnofabric may have reached its more extensive distribution in the Equatorial belt during the Late Ordovician (Jin *et al.* 2012), it became established for the first time in Baltica in the Early Ordovician (Ekdale & Bromley 2003). Burrow systems form multi-level galleries that reach at least 1 m deep (Jin *et al.* 2012). These mazes and networks of variable morphology have been assigned to either *Balanoglossites* or *Thalassinoides* (Fig. 6). As with the similar burrow systems in Cambrian carbonates previously discussed, this bioturbation style may have involved the activity of gallery biodiffusers and regenerators. Regardless of these uncertainties, the presence of deeply penetrative, pervasive, and widespread burrow galleries underscores the significance of bioturbation, suggesting elevated levels of bioirrigation. It has been argued that burrow construction facilitated the establishment of an endobenthos that thrived in these well-oxygenated carbonate platforms (Jin *et al.* 2012).

Palaeogeographic patterns in Ordovician deep-sea colonization

As discussed below, Ediacaran and Cambrian deep marine sediments were essentially stabilized by microbial mats and display ichnofaunas that reflect exploitation of these resources (MacNaughton *et al.* 2000; Orr 2001; Buatois & Mángano 2003). However, this situation changed

dramatically during the Ordovician Radiation with the arrival in the deep sea of new groups of tracemakers, and the first occurrence of graphoglyptid communities (Orr 2001; Uchman 2003, 2004; Buatois *et al.* 2009).

Graphoglyptids are open burrows that are made by organisms that bioirrigate the fine-grained sediment. From an ecosystem engineering perspective, these structures may have increased ventilation and oxygenation in

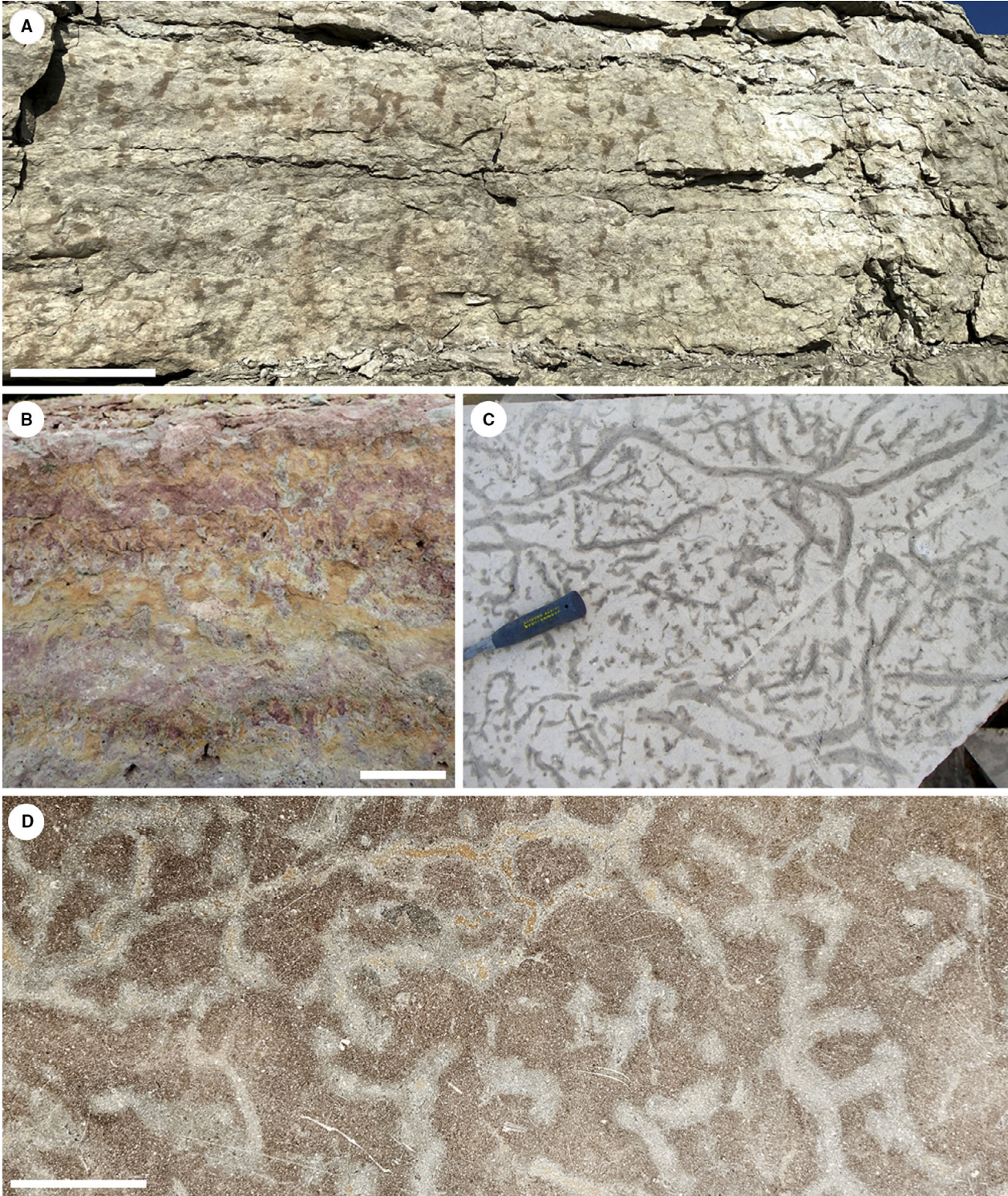


FIG. 6. Pervasive deep-tier bioturbation represented by three-dimensional branching burrows in Ordovician equatorial carbonates. A, general view of bioturbated argillaceous wackestone showing abundant shafts connecting horizontal galleries; Darriwillian, Kõrgekallas Formation, Aru-Lõuna (Kunda-Aru) quarry, Estonia. B, cross-section view of intensely bioturbated limestone, locally showing U-shaped burrow segments; Dapingian, Volkhov Formation, Babino quarry, St Petersburg Region, Russia. C, bedding-plane view of branching burrow systems showing Y-shaped bifurcations; Katian, Selkirk Member, Red River Formation, Gillis Quarries, Garson, Manitoba, Canada; length of hammer is 33.5 cm. D, close-up of horizontal galleries with dominance of T-shaped bifurcations; Darriwillian, Holen Limestone; floor of National Museum, Stockholm. All photographs were taken in the field. Scale bars represent: 1 m (A); 5 cm (B, D).

diffusion-dominated, fine-grained benthic systems (Buatois *et al.* 2023b). These complex burrow systems are most likely made for farming and trapping purposes in an environment characterized by limited food resources (Seilacher 1977; Uchman 2007; Uchman & Wetzel 2011).

Ongoing work plotting occurrences of deep-sea ichnofaunas in the Ordovician, using Gplates, shows that slope and base of slope settings around the Iapetus were first colonized by this new group of tracemakers during the Early Ordovician. A progressive expansion of bioturbators into low latitudes of the Palaeo Tethys facing Gondwana during the Middle Ordovician and into high-latitude, glaciated peri-Gondwanic margins during the Late Ordovician is also apparent. Incidentally, reconstructing the palaeogeographic distribution of deep sea ichnofaunas may help to constrain available models of Ordovician deep-sea oxygenation based on different levels of pCO₂ (Pohl *et al.* 2023). Ichnological evidence shows partial support for models proposing intermediate conditions of pCO₂, as these imply well-oxygenated conditions in the deep-sea areas of Laurentia, Baltica and Gondwana facing the Iapetus Ocean. Even so, oxygen levels should have been higher in the deep sea than envisaged under these values of pCO₂ all around Gondwana to sustain an infauna in the Palaeo Tethys.

Intermediate-term temporal and global spatial scale

The dataset required to unravel patterns at this combination of scales needs to be comprehensive and systematic, implying that all trace fossil determinations must be checked and that a consistent ichnotaxonomic philosophy needs to be adopted. In the same vein, discrete subenvironments need to be standardized. In addition, analyses must first account for variations in the rock record that may be influencing observed patterns, and trade-offs in the resolution of the temporal analysis may be necessary to ensure that identified patterns reflect evolutionary phenomena rather than biases due to the quality of the rock and trace fossil record (Minter *et al.* 2017; Buatois *et al.* 2020; Bowyer *et al.* 2024). In the case of Buatois *et al.* (2020), this involved quantifying the number of both trace fossil-bearing and non-trace fossil-bearing

formations to give the total number of formations as a proxy for rock volume for any given time interval. This enabled assessment of correlations with observed metrics because the measure of just trace fossil-bearing formations is highly likely to be redundant with respect to diversity metrics. This combination of scales of analysis is here illustrated with the study of trace-fossil records from the two main Palaeozoic evolutionary radiations: the Cambrian Explosion and the Ordovician Radiation (Buatois *et al.* 2020), and from the largest mass extinction of all times, the end-Permian mass extinction (Hofmann *et al.* 2015; Cribb & Bottjer 2020; Luo *et al.* 2021).

Bioturbators as ecosystem engineers in the Cambrian Explosion

The extent of the Cambrian Explosion cannot be evaluated without characterizing the Ediacaran ecosystems that preceded this evolutionary event. Shallow marine deposits coeval with deep marine ones containing the Avalon Assemblage (575–560 Ma) are known to contain simple grazing trails (Clarke *et al.* 2024). However, it is the White Sea Assemblage (560–550 Ma) that has been explored in more detail as it represents a more extensive window in which to assess Ediacaran shallow marine ecosystems (Narbonne 1998, 2005; Jensen *et al.* 2006). These deposits are overwhelmingly dominated by simple grazing trails (Gehling 1999; Droser *et al.* 2002a; Jensen 2003; Jensen *et al.* 2006; Mángano & Buatois 2014, 2020; Buatois & Mángano 2016; Buatois *et al.* 2020). In addition, they are host to trace fossils produced by iconic elements of the Ediacara biota, such as *Dickinsonia* and *Kimberella* (Ivantsov & Malakhovskaya 2002; Seilacher *et al.* 2005; Fedonkin *et al.* 2007a; Seilacher & Hagadorn 2010; Sperling & Vinther 2010; Ivantsov 2013; Gehling *et al.* 2014; Buatois & Mángano 2016; Evans *et al.* 2019; Ivantsov *et al.* 2019; Ivantsov & Zakrevskaya 2022). Exploitation of food resources in microbial mats was the dominant feeding strategy evidenced by the ichnofauna, either via non-specialized deposit and detritus feeding, grazing, or osmotrophy (Seilacher & Pflüger 1994; Seilacher 1999; Laflamme *et al.* 2009; Sperling & Vinther 2010; Buatois & Mángano 2012; Mángano & Buatois 2014). All of these

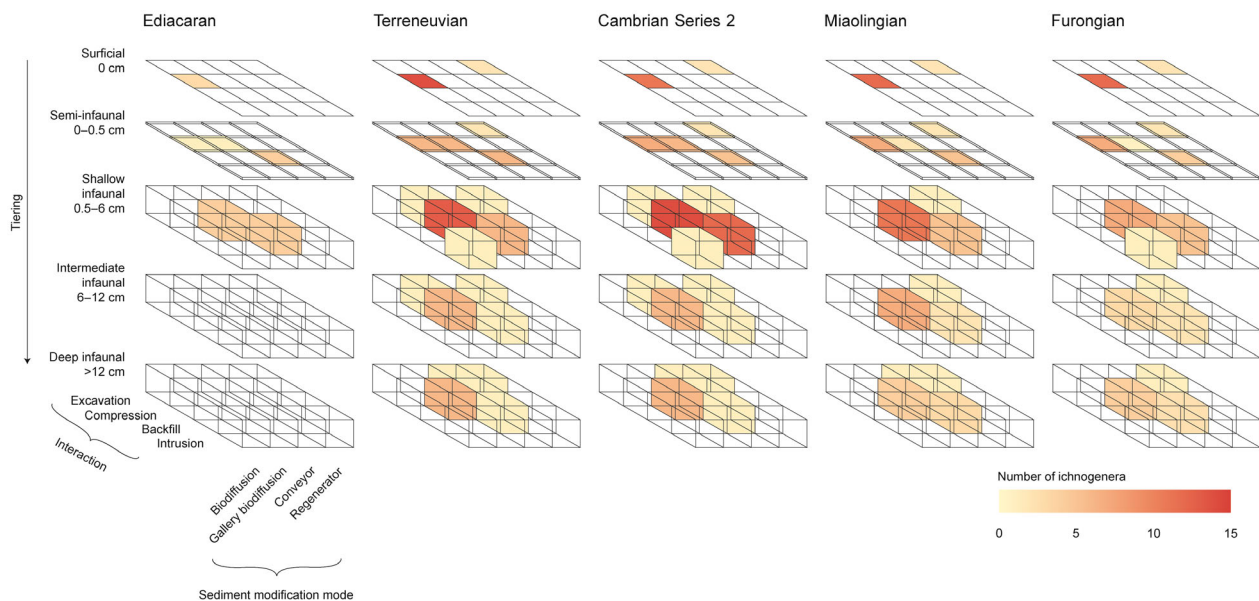


FIG. 7. Ediacaran to Cambrian global trends in ecosystem engineering. The number of ichnogenera within each mode of ecosystem engineering is represented by a heat map. See text for explanation.

Ediacaran trace fossils record surficial to semi-ifaunal activities, being responsible for minimum sediment reworking and, therefore, of very limited impact in terms of ecosystem engineering (Mángano & Buatois 2014; Buatois *et al.* 2020). In the presence of stabilized, relatively firm substrate, compression was the dominant mode of interaction with the substrate (i.e. modes of substrate penetration) and biodiffusion was the main mode of sediment modification. Backfilling and conveying may have been represented by the ichnogenus *Torrowangea*, but this ichnotaxon and other actively infilled burrows are relatively rare. As a result, metrics of alpha and global ichnodiversity, ichnodisparity, modes of life, and styles of ecosystem engineering are rather low (Mángano & Buatois 2014; Buatois *et al.* 2020). This general picture persisted well into part of the time represented by the Nama Assemblage (550–538 Ma). This stage of essentially negligible ecosystem engineering impact by incipient bioturbators represents the initial phase (560–540 Ma) discussed by Mángano & Buatois (2020).

Trace fossil assemblages roughly occurring during the subsequent 540–538 Ma span unquestionably support significant qualitative and quantitative changes in bioturbation. This change in scenario marks the final interval of the Nama Assemblage (second phase in Mángano & Buatois 2020). The main innovations from the perspective of bioturbation are the appearance of more penetrative, simple branching burrows collectively referred to as treptichnids (Jensen *et al.* 2000) and of larger horizontal backfilled burrows represented by the ichnospecies *Parapsammichnites pretzeliformis* (Buatois *et al.* 2018). In terms of feeding

strategies, treptichnids either represent specialized deposit feeding or predation, the latter based on analogies with incipient *Treptichnus pedum*, which are produced by modern priapulids (Vannier *et al.* 2010; Kesidis *et al.* 2019; Turk *et al.* 2024a), whereas *Parapsammichnites pretzeliformis* is most likely to record the activity of a specialized deposit feeder (Buatois *et al.* 2018). These large trace fossils (mean width 0.8 cm, up to 1.1 cm wide) represent semi-ifaunal and shallow-tier occupation, reaching a depth of bioturbation of at least 1 cm. Patches of moderately bioturbated sediment are seen in cross-section for the first time. Regarding styles of ecosystem engineering and modes of interaction with the sediment, treptichnids may represent the earliest example of gallery biodiffusion, whilst *Parapsammichnites* represents uncontroversial evidence of backfilling and conveying, recording the onset of sediment bulldozing. In addition to this increase in diversity in the styles of ecosystem engineering, an increase in the abundance of grazing trails preserved on bedding surfaces is apparent (Cribb *et al.* 2019; Mángano & Buatois 2020; Darroch *et al.* 2021; Turk *et al.* 2022). The appearance of burrows with robust linings (Turk *et al.* 2024b) may have acted as sediment stabilizers as an adaptation to emerging mixground substrates. In short, the last few million years of the Ediacaran are signalled by an increase in the ecosystem engineering impact of bioturbation (Cribb *et al.* 2019; Darroch *et al.* 2021). However, this is still far from Cambrian levels, as indicated by metrics of alpha and global ichnodiversity, ichnodisparity, modes of interaction with the sediment, and styles of ecosystem engineering (Fig. 7) (Mángano & Buatois 2014; Buatois *et al.* 2020).

The picture from deep marine environments is more uncertain due to a rather fragmentary record of these settings. Putative, cnidarian-grade trace fossils have been proposed (Liu *et al.* 2010), but overall evidence of animal motility in the Avalon (575–560 Ma) deep marine environments is rather limited (Menon *et al.* 2013). Deep marine deposits of White Sea Assemblage age were dominated by similar simple grazing trails to those recorded in coeval shallow marine deposits (Narbonne & Hofmann 1987; Narbonne & Aitken 1990; Vidal *et al.* 1994; MacNaughton *et al.* 2000; Jensen *et al.* 2007; Hofmann & Mountjoy 2010; Carbone & Narbonne 2014; Buatois & Mángano 2016). The impact of bioturbation in terms of ecosystem engineering may have been negligible in deep marine systems. Notably, there is no available evidence supporting a scenario in which the evolutionary innovations of the terminal Nama Assemblage reached deep-sea environments.

Cambrian ichnological data show three distinct phases: (1) Fortunian (538–529 Ma); (2) Cambrian Stages 2 to 4 (529–509 Ma); and (3) Miaolingian–Furongian (509–485 Ma) (Buatois *et al.* 2020). The Fortunian is signalled by the most remarkable increase in both global and alpha ichnodiversity and ichnodisparity in the history of life (Mángano & Buatois 2014, 2020; Buatois *et al.* 2016, 2020; Buatois & Mángano 2018). Innovations are particularly well recorded in shallow marine environments, where this increase was accompanied by an equally dramatic rise in the variety of feeding strategies, styles of ecosystem engineering, and modes of sediment modification (Buatois *et al.* 2020). In addition to non-specialized and specialized detritus and deposit feeding, predation clearly emerged, but mobile and sessile suspension feeders remained considerably rare. Possible early evidence of chemosymbiosis is represented by the ichnogenera *Chondrites* (Webby 1984) and *Trichichnus* (Laing *et al.* 2019; Gougeon *et al.* 2023), the latter rather widespread in offshore to shelf settings. Also, farming strategies may have been present as indicated by the ichnogenera *Dendrohaphe* (Jensen & Mens 1999) and *Gyrolithes* (Laing *et al.* 2018). In terms of occupation of the endobenthic ecospace, colonization expanded down reaching up to 6 cm in penetration depth. However, bioturbation intensity continued to be low to moderate (Mángano & Buatois 2014). Of the four modes of interaction with the substrate, three (compression, backfill and excavation) became common. In contrast to the Ediacaran in which whole modes of sediment modification were represented by just a few ichnotaxa or even a single ichnotaxon, several representatives of each of the three categories recognized (biodiffusion, gallery biodiffusion, conveying) are present in the Fortunian (Fig. 7) (Buatois *et al.* 2020). Overall, metrics of alpha and beta ichnodiversity, ichnodisparity, modes of life and styles of ecosystem

engineering showed a remarkable increase in comparison with Ediacaran levels. In contrast, deep-sea environments have experienced a lower increase in these metrics (Buatois *et al.* 2020). However, the signature of the Cambrian Explosion is clearly displayed by the presence of arthropod trackways and the complex burrow system *Oldhamia* (Churkin & Brabb 1965; Lindholm & Casey 1989 1990; Sweet & Narbonne 1993; Orr 2001; Buatois & Mángano 2003; Seilacher *et al.* 2005; Herbolch & Verniers 2011). Compression was the dominant mode of interaction with the substrate, whereas biodiffusion and gallery biodiffusion were the main styles of sediment modification (Buatois *et al.* 2020). Notably, an Ediacaran-style ecology based on the exploitation of microbial mats persisted in the Fortunian (Fig. 8) (Dornbos *et al.* 2004; Buatois *et al.* 2014). This was accompanied by widespread firm substrates present close or at the sea floor during most of the Fortunian (Droser *et al.* 2002b, 2004).

The Cambrian Stages 2 to 4 phase is complex in terms of global and alpha ichnodiversity trajectories, with Stage 2 showing no major change and Stages 3 and 4 displaying a second significant burst of ichnodiversity, which was accompanied by a more modest increase in ichnodisparity (Mángano & Buatois 2014; Buatois *et al.* 2016, 2020). The signature of this phase is a remarkable change at ecosystem scale, which has been traditionally referred to as the agronomic revolution (Fig. 8) (Seilacher & Pflüger 1994; Seilacher 1999; Mángano & Buatois 2014, 2017). Non-specialized and specialized detritus and deposit feeding, predation, and chemosymbiosis continued to be widespread. Suspension feeding became the dominant feeding strategy in nearshore, agitated waters, as evidenced by profuse vertical burrows, typically forming *Skolithos* piperock (Hallam & Swett 1966; Droser 1991; Davies *et al.* 2009; Desjardins *et al.* 2010; Fang *et al.* 2012). Possible early examples of farming are suggested by the presence of the ichnogenus *Zoophycos* (Jensen 1997; Grazhdankin *et al.* 2020), as well as networks (Crimes & Anderson 1985; Paczeńska 1985, 1996) and possibly meandering graphoglyptids (Stachacz 2016). The mid and deep tiers were occupied for the first time, and maximum burrowing depths of up to 1 m were recorded in nearshore areas (Hallam & Swett 1966; Davies *et al.* 2009) and up to 57 cm in the offshore (Gougeon *et al.* in press). Increased bioturbation depth was accompanied by a significant rise in the intensity of bioturbation, with thorough biogenic mixing of the sediment under appropriate environmental conditions (e.g. Clausen & Vilhjálmsson 1986; McIlroy & Logan 1999; Loughlin & Hillier 2010; Desjardins *et al.* 2012; Mángano & Buatois 2014, 2016, 2017; Mazurek 2014; Stachacz 2016; Herbers *et al.* 2016; Gougeon *et al.* 2018). The Fortunian to Cambrian Age 2 transition was signalled by the

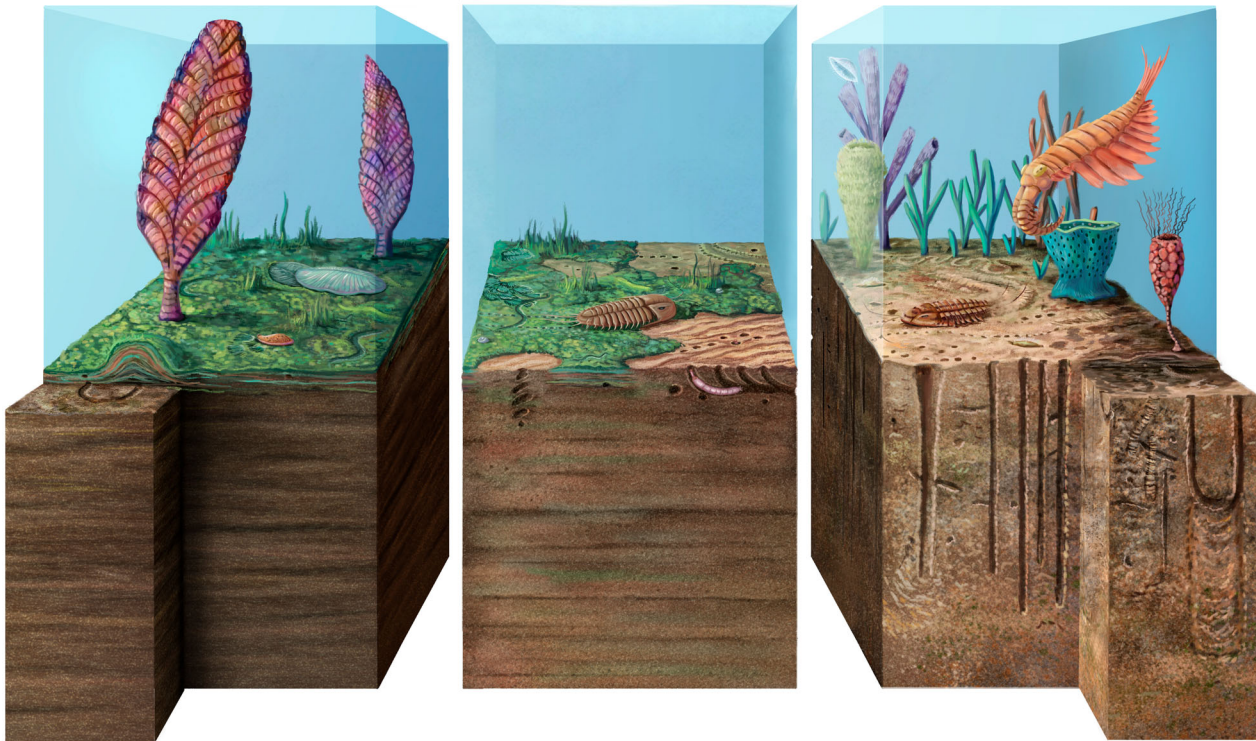


FIG. 8. The agronomic revolution revisited. The Fortunian represents an intermediate stage between the Ediacaran-style matgrounds on the left and the Cambrian-style mixgrounds on the right, characterized by the persistence of a microbial mat ecology and the appearance of new body plans. Illustration by Kaitlin Lindblad after Seilacher (1999) inspired by Peter Trusler's reconstruction in Fedonkin *et al.* (2007b).

appearance of a modern-style vertical zonation of marine sediments, as evidenced by the presence of discrete trace fossils emplaced in the transition zone cross-cutting undifferentiated mottling characteristic of the mixed layer (Gougeon *et al.* 2018). Compression, backfill and excavation continued to be widespread modes of interaction with the substrate (Buatois *et al.* 2020). Biodiffusion, gallery biodiffusion and conveying are all represented by an even larger number of ichnotaxa than in the Fortunian. In particular, the impact of gallery biodiffusors increased, as these became more diverse and abundant as shown by the increase in diversity and density of suspension-feeding burrows. Notably, no major innovations are apparent in the deep sea, with ichnofaunas essentially identical to those of the Fortunian, other than rare occurrences of radial structures (Gingras *et al.* 2011), regular networks (Jensen & Palacios 2006), and putative irregular networks (Hofmann *et al.* 1994), which may record early examples of farming feeding strategies. Overall, there is a clear pattern of increased habitat segregation in the aftermath of the agronomic revolution (Meek *et al.* 2023).

The Miaolingian–Furongian timespan shows a decrease in global ichnodiversity and ichnodisparity. The same

feeding modes as those revealed by earlier ichnofaunas are apparent. However, a decrease in the abundance of *Skolithos* piperock has been noticed (Fang *et al.* 2012), which suggests a lower contribution by suspension feeders. No major changes in terms of depth and extent of bioturbation are detected. Indeed, modes of life and styles of ecosystem engineering show a decrease during the Miaolingian, reaching minimum values during the Furongian when all marine environments are considered together (Fig. 7) (Buatois *et al.* 2020). In contrast to the late early Cambrian, the middle and late Cambrian display a decrease in most ichnological proxies in the offshore regions as well, arguing for more widespread anoxic events. This pattern is consistent with the scenario of recurrent biotic crises commonly attributed to oxygen depletion (Gill *et al.* 2011; Saltzman *et al.* 2015; Chen *et al.* 2023). The decrease in metrics during the Miaolingian is also expressed in deep marine environments. However, the scarcity of well-dated Furongian deep marine strata prevents further elaboration on this trend. In short, ichnological data are consistent with body-fossil data in showing that by the end of the early Cambrian, the Cambrian Explosion was essentially over (Mángano & Buatois 2014).

Bioturbators as ecosystem engineers during the Ordovician Radiation

Defining phases for the Ordovician (485–443 Ma) is less straightforward as changes seemed to have occurred more gradually and at a more regular pace rather than in discrete time intervals. After a substantial drop during the Miaolingian–Furongian, global ichnodiversity experienced a significant rebound through the Ordovician (Mángano & Droser 2004; Buatois *et al.* 2016, 2020; Mángano *et al.* 2016; Buatois & Mángano 2018). Although this increase in ichnodiversity is evident in both shallow and deep marine environments, it is more pronounced in the latter. In turn, global ichnodisparity only shows a modest increase for bioturbation structures, although bioerosion structures do show a significant rise (Wilson & Palmer 2006; Buatois *et al.* 2016; Mángano *et al.* 2016). In shallow marine environments, the same feeding strategies identified in the Cambrian are present. However, farming seems to have become increasingly rare in these settings, only indicated by the presence of *Zoophycos* (e.g. Fillion & Pickerill 1984; Mikuláš 1999; Mángano & Buatois 2003; Clark-Lowes 2005; Meischner *et al.* 2020; Bokr *et al.* 2021). Also, some specialized strategies most likely involving chemosymbiosis became more common, as indicated by the widespread presence of *Chondrites*, which shows a progressive increase in the number of occurrences through the Ordovician (Buatois *et al.* 2020). In addition, this feeding mode is also recorded by the appearance of several bioerosion and bioturbation ichnogenera, namely *Fascifodina*, *Pragichnus* and *Solemyatuba* (Osgood 1970; Seilacher 1990; Mikuláš 1997; Mángano & Buatois 2003; Buatois *et al.* 2020). No increase in maximum depth of bioturbation is apparent, but pervasively mixed sediments in both siliciclastic and carbonate marine environments in the absence of significant stressors have been extensively recorded (e.g. Bayet-Goll & Neto de Carvalho 2016, 2017; Zheng *et al.* 2018; Dorador *et al.* 2019; Bokr *et al.* 2021). Ichnotaxa metrics in offshore environments show a long-term trend of subtle increase, albeit punctuated by an equally subtle decrease during the Middle Ordovician (Buatois *et al.* 2020).

Notably, as discussed above, it is in deep marine environments where the Ordovician Radiation displays some of its most remarkable evolutionary innovations (Orr 2001; Uchman 2003, 2004; Buatois *et al.* 2009). Global ichnodiversity and ichnodisparity show a sustained increase in these settings through the whole period (Mángano & Droser 2004; Buatois *et al.* 2016; Mángano *et al.* 2016; Buatois & Mángano 2018). A progressive turnover in the dominant feeding modes is a significant milestone in the Ordovician deep sea. The undermat mining trace fossil *Oldhamia* has not been recorded in deep marine deposits after the Cambrian. Overall, the

association of trace fossils with microbial mats in Ordovician deep marine deposits is not as significant as in the Cambrian and was essentially restricted to patches of microbially stabilized sediment (Buatois *et al.* 2009; Bayet-Goll *et al.* 2022). Farming feeding modes, which seem to have originated in shallow water, gradually established a stronghold in the deep sea, as shown by well-supported evidence of the presence of the main architectural designs of graphoglyptids, namely regular networks, delicate spiral burrows, guided meandering, uniramous meanders, and radial patterns (Uchman 2003, 2004; Mángano & Droser 2004; Mángano *et al.* 2016). However, microbial mat exploitation was not directly replaced by farming as the main strategy. Instead, deposit feeding was dominant in the deep sea during the Early to Middle Ordovician, with farming only reaching significant levels by the Late Ordovician to early Silurian (Orr 2001; Uchman 2003; Mángano *et al.* 2016). Parallel to these innovations was a marked increase in depth of bioturbation, as reflected by the colonization of deep tiers, with up to 40 cm of penetration depth recorded for some burrows (Pickerill & Williams 1989; Orr 2003). As a result of these innovations, all ichnotaxa metrics also show a marked increase through the Ordovician (Buatois *et al.* 2020).

Bioturbation and the end-Permian mass extinction

The Permo-Triassic mass extinction can also be scaled-up to the global spatial scale (Cribb & Bottjer 2020). Data on shallow marine trace fossil assemblages were compiled from the literature at the stage level from the beginning of the Permian to the mid-Triassic, and the multidimensional ecosystem engineering cubes and sum of ecosystem engineering impacts across ichnotaxa were characterized for each of these intervals. Results demonstrated that burrow tiering depth changes from primarily intermediate to deep infaunal tiers during the Permian to shallow and semi-infaunal tiers in the Triassic (see also Buatois & Mángano 2011b; Hofmann *et al.* 2015 and Luo *et al.* 2021); however, the number of modes of ecosystem engineering and ecosystem engineering impact did not decrease, and instead persisted, across the boundary (Cribb & Bottjer 2020). Still, data are limited for certain stages, with no trace fossil assemblages from the Roadian and Capitanian and information for some stages only from single papers. Interestingly, a set of characteristics observed in trace fossil suites from the earliest Triassic (e.g. common preservation of shallow-tier burrows with bioglyphs) indicates extensive development of firmgrounds close to or at the sediment–water interface, which has been taken as evidence of the collapse of the soupy mixed layer (Buatois & Mángano 2011b; Hofmann *et al.* 2015).

Long-term temporal and regional spatial scale

This combination of scales has hardly been used in the analysis of bioturbation. This approach is complicated because of changes in the configuration of continents and oceans through time. Long-term temporal and regional scales are here illustrated with a synthesis of the role of bioturbation in high-latitude settings through the Phanerozoic.

Trends in bioturbation impact in marine polar environments

This is a topic of central significance as global warming is profoundly and rapidly affecting community structure and ecosystem functioning in several ways, including poleward shifts of species from temperate areas (Bianchi *et al.* 2021) and seasonal variations in sea ice extent affecting food webs and benthic–pelagic coupling (Solan *et al.* 2020), with food resource availability exerting a strong control on the type of bioturbation. Traces of deposit feeders (e.g. *Scolicia*) are the most abundant during times of seasonal sea-ice cover and rich food delivery but those of chemosymbionts (e.g. *Chondrites*) are dominant during conditions of more severe sea ice cover, limited food supply, and restricted bottom water (Singh *et al.* 2023). Deep-tier burrowing by chemosymbiont thyasirid bivalves is pervasive in temperate fjords with a sill that restricts water circulation, resulting in extensive dysoxia (Dando & Southward 1986; Schatz *et al.* 2013). Latitudinal comparisons of biogenic structures in marine environments indicate that high-latitude cold settings are dominated by structures produced by molluscs and annelids (Goldring *et al.* 2004). Extensive bioturbation by ophiuroids, worms and protobranch bivalves has been documented along the depositional profile of Arctic fjords resulting in the total obliteration of the primary fabric (Schatz *et al.* 2013).

Evaluation of changes in type and intensity of bioturbation in polar settings through geological time is complicated due to the uneven distribution of glaciomarine and associated deposits in the stratigraphic record. Also, long-term alternation between warm greenhouse and colder icehouse states through geological time has resulted in highly contrasting ecological conditions at high-latitude polar regions (Zalasiewicz & Williams 2021). Cryogenian snowball events and the Ediacaran Gaskiers glaciation preceded the onset of bioturbation. Ichnofossil-bearing glaciomarine deposits originally dated as 585 myr old were subsequently demonstrated to be late Palaeozoic (Gaucher *et al.* 2013; Verde *et al.* 2022). Trace fossils have not been recorded so far in direct association with any of the deposits corresponding to the younger Ediacaran glacial events that, in contrast to the Cryogenian ones, are

restricted to mid to high latitudes (Niu *et al.* 2024; Sun *et al.* 2024).

The earliest evidence of bioturbation in polar environments corresponds to low-diversity suites of simple trace fossils in Gondwanan Hirnantian glacial deposits accumulated near the south polar ice sheet in North Africa (e.g. Turner *et al.* 2005; Le Heron *et al.* 2010; Ghienne *et al.* 2023). Given the scarcity and limited variability of the trace fossils recorded, overall impact of bioturbation was probably very low and restricted to shallow tiers, mostly involving the backfill mode of penetration and conveyor mode of sediment modification. This is in sharp contrast to the underlying Ordovician preglacial deposits in these high latitudes, which are host to relatively diverse trace fossil suites (e.g. Le Heron & Howard 2010, 2012; Ghienne *et al.* 2023). Notably, a latitudinal gradient in bioturbation intensity and diversity is apparent as reflected by trace fossil assemblages in Hirnantian deposits accumulated in ice-marginal shallow marine environments adjacent to a separate ice sheet in South Africa (Davies *et al.* 2020) and in peri-Gondwanic terranes (Brenchley & Štorch 1989; Mikuláš 1992). The ecosystem engineering role of bioturbation in these regions somewhat resembles that of other contemporaneous shallow marine environments in more temperate regions.

No detailed ichnological documentation is available from Late Devonian glaciated margins, but there are several studies on the ichnology of fjords and associated glaciomarine areas in Gondwana during the Late Palaeozoic Ice Age or LPIA (e.g. Buatois & Mángano 1992; Buatois *et al.* 2006, 2010; Bhattacharya & Bhattacharya 2007; Sarkar *et al.* 2009; Schatz *et al.* 2011; Netto *et al.* 2012; Alonso-Muruaga *et al.* 2018). The impact of bioturbation in these settings was dependent on associated salinity conditions. Simple grazing trace fossils and arthropod trackways recording a freshwater epibenthos to very shallow endobenthos were dominant in inner regions of late Palaeozoic Gondwanan fjords at the time of deglaciation (Buatois & Mángano 1992; Buatois *et al.* 2006, 2010; Alonso-Muruaga *et al.* 2012, 2018, 2020; Netto *et al.* 2012; Isbell *et al.* 2023). This association represents freshwater conditions due to extreme water discharge from melting of the continental ice masses (Buatois *et al.* 2006, 2010). The role of bioturbation from the perspective of ecosystem engineering under these conditions is indistinguishable from that of coeval lacustrine environments and was limited to very shallow tiers (Minter *et al.* 2017). The trace fossil content of the brackish-water portion of late Palaeozoic Gondwanan fjords is poor and dominated by a few monospecific to paucispecific suites of simple burrows and bilobate structures (Schatz *et al.* 2011; Alonso-Muruaga *et al.* 2012). In places, bilobate structures recording the activities of small arthropods were directly associated with ice rafted debris (Schatz *et al.* 2011).

The general scarcity of bioturbation in these deposits suggests limited impact in terms of ecosystem engineering. Overall, ice-marginal shallow-marine successions show a clear trend of increased intensity of bioturbation and diversity of trace fossils parallel to climatic amelioration (Bhattacharya & Bhattacharya 2007; Alonso-Muruaga *et al.* 2013). In fact, bioturbation was absent near the ice masses at times of repeated advances and retreats of the ice sheet. During final retreat of the ice sheet, deposits became more intensely bioturbated and moderately diverse trace fossil assemblages were recorded (Bhattacharya & Bhattacharya 2007; Sarkar *et al.* 2009; Luo *et al.* 2017). Still, the small size of trace fossils and their sporadic distribution underscore the role of multiple stressors in late Palaeozoic polar settings, such as dilution of normal marine salinity due to melt-out freshwater discharge, times of dysoxia, and high sedimentation rates (Bhattacharya & Bhattacharya 2007; Sarkar *et al.* 2009). A wider variety of modes of penetration in the sediment and styles of ecosystem engineering is apparent in these deposits. However, the sparse distribution of bioturbation represents a marked departure from assemblages at lower latitudes and suggests comparatively smaller impact in terms of ecosystem engineering.

The Mesozoic represents the longest period of warm conditions during the Phanerozoic, albeit punctuated by short-lived cold periods (Donnadieu *et al.* 2011; Landwehrs *et al.* 2021). Accordingly, Mesozoic successions formed in high latitudes provide a window to evaluate the impact of bioturbation in polar regions during greenhouse conditions. A recent study by Leszczyński *et al.* (2023) documented in detail the ichnofauna of the Early Cretaceous Svalbard shelf. These authors recorded high ichnodiversity in offshore to lower shoreface deposits. Intensity of bioturbation is particularly high in those sediments accumulated in the offshore transition. Despite the overall high ichnodiversity, Leszczyński *et al.* (2023) regarded this ichnofauna as impoverished compared to coeval ones in low latitudes. The limiting environmental factor on the benthos in these polar regions during greenhouse conditions was the high frequency and magnitude of storms. Periodic invasions of cold polar water in the Svalbard shelf may have played a role, most notably being deemed responsible for the scarcity of ichnotaxa (e.g. *Ophiomorpha*) produced by typical elements of lower latitudes, such as callianassid crustaceans (Leszczyński *et al.* 2023). Worms and, to a lesser extent bivalves, other crustaceans and sea anemones, are possible producers. Regardless, in comparison with Palaeozoic polar regions under icehouse conditions, the variety of styles of ecosystem engineering in the sediment is significantly higher in this high-latitude area characterized by overall warmer conditions.

Information from Cenozoic polar areas indicates a slight increase in ichnodiversity and a remarkable extent

of bioturbation in deposits formed under a wide range of water depth conditions in comparison with those of previous icehouse conditions (e.g. Eyles *et al.* 1992; Uchman & Gaździcki 2010; Fielding 2018). A sedimentological study of cores taken in McMurdo Sound, Antarctica, spanning from the Eocene to the Quaternary allows evaluation of changes in bioturbation at the onset of the Cenozoic Ice Age (Fielding 2018). A lack of systematic ichnological analysis, however, prevents a comprehensive assessment of styles of ecosystem engineering. Eocene preglacial deposits and early Oligocene deposits that indicate the onset of the glaciation are variably bioturbated. Specifically, mudstone intercalated with dispersed gravel is intensely and diversely bioturbated (Fielding 2018). Oligocene deposits corresponding to the growth of the East Antarctic Ice Sheet show a pattern of progressive decrease in ichnodiversity and intensity of bioturbation, reflecting the increased importance of stressors. Expansion of the East Antarctic Ice Sheet took place during the late Oligocene to Early Miocene, resulting in the dominance of diamictite under conditions that were not conducive to the preservation of trace fossils. Moderately diverse ichnofaunas and fluctuating intensities of bioturbation characterize the subsequent Miocene Climatic Optimum, with suites mostly controlled by freshwater discharge in estuarine and deltaic settings (Fielding 2018). Despite these stressors, this time was signalled by a wider variety of styles of ecosystem engineering, particularly conveyors and gallery biodiffusers, as well as occupation of multiple tiers. The Middle to Late Miocene expansion of the East Antarctic Ice Sheet was characterized by diamictite deposition under dominant conditions of permanent ice cover that were detrimental for benthic activity (Fielding 2018). Overall warming during the Pliocene paralleled an increase in the degree of bioturbation and the occurrence of complex trace fossils, such as robust *Zoophycos* (Miller *et al.* 2009). Finally, no published records of bioturbation are available from deposits formed during the Quaternary expansion of the East and West Antarctic Ice Sheets. To sum up, alternation of times of glacial expansion and climatic amelioration during the Cenozoic seem to have corresponded to trends of decreased and increased intensity of bioturbation and ichnodiversity, respectively. Overall, ichnological information from polar areas in the Arctic and Antarctica (e.g. Eyles *et al.* 1992; Uchman & Gaździcki 2010) suggests that the Cenozoic ice age represents the onset of the polar modern fauna.

Long-term temporal and global spatial scale

As with the intermediate temporal scale and global scale, the large end of this combination of scales (i.e. spatial and temporal) requires the compilation of comprehensive

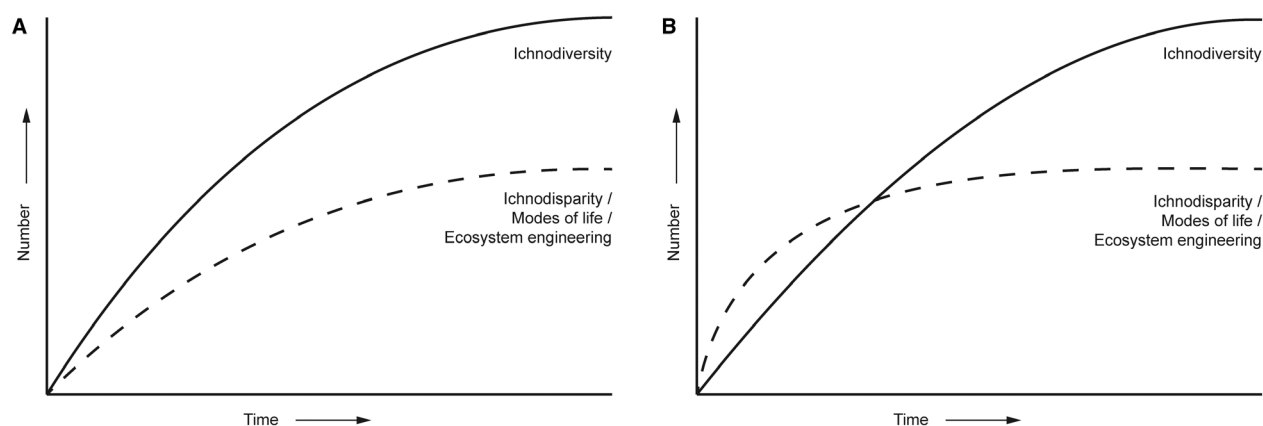


FIG. 9. Hypothetical models for trends in ichnodiversity, ecospace occupation, and ecosystem engineering during the Palaeozoic invasion of the land. A, model of coupled ichnodiversity and ichnodisparity. B, early burst model of ichnodisparity.

and systematic datasets. This combination of scales of analysis is here illustrated with the study of trace-fossil records of Palaeozoic terrestrialization (Minter *et al.* 2017) and of marine environments during the Mesozoic Marine Revolution (Buatois *et al.* 2016, 2022a).

Palaeozoic terrestrialization

In the study by Minter *et al.* (2017), palaeoenvironments were standardized using a matrix that comprises nine categories. Three broad environments, coastal, alluvial and lacustrine, were considered. In turn, these were subdivided into permanently subaqueous, transitional and subaerial, to accommodate ecological preferences of the tracemakers. Potential effects of rock record bias were assessed by testing for relationships between ichnological metrics and estimates of rock volume obtained from Ronov *et al.* (1980), which found that a trade-off of analysis at the temporal resolution of the period was necessary. Minter *et al.* (2017) showed that the Palaeozoic colonization of the continents was signalled by repeated early bursts of high levels of ichnodisparity, ecospace occupation and ecosystem engineering that preceded maximal ichnodiversity (Fig. 9). Similarities across different environments in the types of behaviours involved, modes of life, and styles in which bioturbators impacted their environments were interpreted as resulting from constraints in the form of ecological opportunities or genetic potential for innovation that affected the possibilities for behavioural and ecological diversification. A trend of expansion in the colonization of underutilized ecospace, from marginal marine environments to alluvial settings, deserts and lake margins, culminating in permanent subaqueous portions of lacustrine basins, is apparent (Buatois & Mángano 1993; Buatois *et al.* 1998, 2022b;

Minter *et al.* 2017; Shillito & Davies 2020, 2021). With the colonization of each of these new terrestrial environments, there was relatively rapid infilling of available ecospace, followed by diversification of behavioural themes as manifested by trace fossil architectural designs, and then diversification of ichnogenera with the already established ecospace and behavioural repertoires (Minter *et al.* 2017).

Trends in bioturbation in marine environments during the Mesozoic Marine Revolution

At present, a comprehensive dataset of characteristics, including the ability to quantify effects of the rock record, like those outlined previously for the analysis at a global scale for the evolutionary breakthroughs during the Ediacaran–Ordovician interval (Buatois *et al.* 2020), is not available for the rest of the Phanerozoic. However, a compilation of ichnogenetic stratigraphic ranges shows that, in addition to the Cambrian Explosion and the Ordovician Radiation, the Mesozoic Marine Revolution is also revealed by an increase in diversity of trace fossils (Buatois & Mángano 2016, 2018). This is significant as these three major marine radiations have all been defined based on the analysis of body fossils, showing a congruence in the diversity trajectories obtained from both sources of data. Each of these events implies the appearance of a new cast of dominant bioturbators and significant innovations in ecosystem engineering, allowing the reconstruction of trends in bioturbation in marine environments through geological time.

Preliminary information suggests that several innovations and breakthroughs were linked with the onset of the Mesozoic Marine Revolution (Buatois *et al.* 2016). In contrast to the Cambrian Explosion and the Ordovician

Radiation that are here regarded as of intermediate temporal scale and global scale, the Mesozoic Marine Revolution was a protracted process that clearly falls within our long-term scale, which has led to questioning the appropriateness of the term 'revolution' in this case (Lucas & Hunt 2023).

Based on the available ichnological information on this event, four main aspects are here regarded pertinent in terms of the role of bioturbators as ecosystem engineers. First, extensive colonization of the ultra-deep tier (depths below 1 m; Mángano & Buatois 2014) seems to have been the result of the Jurassic radiation of decapod crustaceans, particularly callianassids, followed by periodic bursts in diversification during the rest of the Mesozoic and in the Cenozoic (Förster 1985; Schweitzer 2001; Swen *et al.* 2001; Klompmaker *et al.* 2013; Schweitzer & Feldmann 2015). Trends in diversification of decapod crustaceans overall correlate with changes in abundance and richness of burrow galleries that are typically attributed to this group of burrowers (Carmona *et al.* 2004). Crustacean burrows, such as *Ophiomorpha*, have been recorded penetrating well below the 1 m mark in post Palaeozoic deposits (e.g. Seilacher 1962). This is consistent with observations from modern environments as shown, for example, by up to 3 m deep burrows by the shrimp *Axius serratus* (Pember-ton *et al.* 1976).

Second, evidence of regenerators (i.e. burrowing resulting in the relocation of sediment from below to the surface that becomes available for transportation by physical processes; François *et al.* 2002) in Palaeozoic rocks is somewhat uncertain. Fiddler crabs are the archetypal example (François *et al.* 2002; Aschenbroich *et al.* 2017). The fossil record of this group is remarkably patchy, but its divergence may be traced back in time as far as the Cretaceous (Gibert *et al.* 2013). The ichnogenus *Psilonichnus*, consisting of dominantly vertical, cylindrical, unlined, J, Y or U-shaped burrows, has commonly been attributed to upogebiid shrimp or ocypodid crabs (Nesbitt & Campbell 2002, 2006). This ichnogenus is known from the Late Jurassic onwards (Fürsich 1981), signalling the rise of regenerators as key ecosystem engineers in Mesozoic shallow marine environments.

Third, the rise to dominance of the Modern Evolutionary Fauna implies a marked increase in burrowing efficiency, a trend already identified by Thayer (1979, 1983) in his pioneering studies on the biological disturbance caused by sediment bulldozers and supported by more recent reviews (Buatois *et al.* 2016). These highly mobile bioturbators can manipulate sediment while burrowing, crawling and feeding. Among this, we may list decapod crustaceans, clypeasteroid echinoderms, irregular echinoids, tellinacean bivalves, protobranch bivalves and arenicolid polychaetes, most of which have an extensive ichnological record linked to the Mesozoic Marine Revolution.

Fourth, increased compartmentalization of the endobenthic ecospace is a signature of the Mesozoic Marine Revolution, particularly since the Early Jurassic (Buatois *et al.* 2022a). By using the ichnoguild concept, a reconstruction of how the different components of the endobenthos have exploited different niches within the sediment can be attained. Comparison of ichnoguilds in offshore settings from the Triassic to the Jurassic indicates that the Early Jurassic was a critical time for infaunalization, as revealed by an increase in the maximum number of ichnoguilds per tier, of ichnotaxa per ichnoguild, and of ichnoguilds per community (Buatois *et al.* 2022a). One of the implications of this study is that the post-Palaeozoic endobenthic ecospace was packed with different species, therefore arguing against competitive exclusion. The degree of niche partitioning seen in Early Jurassic offshore settings is remarkable and approaches Cenozoic levels (Carmona *et al.* 2012).

DISCUSSION & PERSPECTIVES

The significance of bioturbation as a driving force in the history of the biosphere as well as its importance for the health of modern ecosystems is now widely accepted (Seilacher 1999; Solan *et al.* 2004; Nogaro *et al.* 2009; Mángano & Buatois 2014; Butterfield 2018). However, the ways in which we can reconstruct and quantify how the work of animals has affected Earth history is extremely challenging and requires the joint efforts of different scientific communities implementing diverse conceptual frameworks and methodological approaches. Regardless of the caveats, the ichnological toolbox has significantly expanded since the early days of the field, and it holds plenty of potential to yield insights into the role of bioturbation in deep-time ecosystem engineering. In the same vein, the trace-fossil record is a large repository of valuable information that may be analysed, considering both constraints and potential, from the perspective of ecosystem engineering.

Analysing bioturbation from this perspective allows ichnology to view the trace-fossil record not just through the lens of animal responses to environmental factors, but through the active role of bioturbators in modifying their environment and interacting with other organisms in the community. From this perspective, the earliest significant effects of bioturbation took place by the very end of the Ediacaran with the onset of penetrative burrowing. Prior to this time, producers of grazing trails seem to have coexisted with the Ediacara biota without a net effect in ecosystem functioning, having a marginal role in modulating resources and biogeochemical cycles. In contrast, bioturbation by the terminal Ediacaran mobile bilaterian benthos generated significant reworking of the substrate

facilitating not only particle advection, but also the incipient irrigation of the substrate. This initial phase of penetrative bioturbation may have contributed to the decline in diversity of the Ediacara biota (Laflamme *et al.* 2013; Darroch *et al.* 2015, 2018, 2021, 2023; Muscente *et al.* 2018). The emergence of sediment bulldozers must have been detrimental particularly for the sessile representatives of the Ediacara biota, as well as for mat-forming microbial communities. Notably, *Parapsammichnites* is found in deposits lacking body fossils and microbially induced sedimentary structures, further supporting the hypothesis of mutual exclusion (Buatois *et al.* 2018). Accordingly, it is not the mere appearance of bilaterians, but most likely the emergence of an abundant mobile benthos capable of disturbing and modifying the sediment that represents the onset of ecosystem engineering by bioturbators (Buatois & Mángano 2016). In this scenario, the onset of sediment bulldozing at the very end of the Ediacaran has been regarded as the earliest evidence of trophic group amensalism (Buatois *et al.* 2018). Also, the occurrence of treptichnids may represent an incipient attempt at bioirrigation, promoting oxygenation of the sediment (Cribb *et al.* 2019). Neoichnological work (Turk *et al.* 2024a) and future computational fluid dynamics simulation models will enlighten our understanding on the effects of these early probing systems on substrate conditions.

Although the last few million years of the Ediacaran represented the prelude of the Cambrian Explosion (Valentine 2002; Schiffbauer *et al.* 2016; Buatois & Mángano 2016), it is during the Fortunian that most of the 'bauplans' (i.e. architectural designs) of bioturbation structures made their appearance in the fossil record (Mángano & Buatois 2014). This increase in ichnodisparity reflects the appearance in shallow marine environments of a cast of characters that is not clearly revealed by the earliest Cambrian macrofossil record, such as arthropods, priapulids, flatworms, nematodes, polychaetes and, more speculatively, enteropneusts and phoronids (Mángano & Buatois 2020). The presence of many of these groups is also reinforced by small shelly fossil (SSF) (Shao *et al.* 2015; Devaere *et al.* 2021; Kono *et al.* 2021) and small carbonaceous fossil (SCF) evidence (Slater *et al.* 2018; Slater & Willman 2019). It has been argued that this emerging benthos may have promoted the creation of niches that were effectively occupied later in the Cambrian (Buatois *et al.* 2020).

Articulation of ichnological datasets across a wide spectrum of spatial and temporal scales illustrates some of the challenges in analysing bioturbation in deep time from the perspective of ecosystem engineering. For example, extrapolation from the local to the global extent is typically unsupported. Exploration of palaeogeographic patterns is still in its infancy (Mángano & Buatois 2011).

Analysis of global trends cannot be done in the absence of systematic compilation of ichnological datasets that are internally consistent on taxonomic grounds. Moreover, caution should be made in putting too much weight on trends based solely on degree of bioturbation, as it is insufficient to extract significant palaeobiological information or explore the ecological attributes of trace fossil associations. Most notably, there is a surprising absence of studies that integrate in detail geochemical and ichnological sampling within robust palaeoenvironmental models and sequence stratigraphic frameworks. Delineating geochemical gradients linked to discrete bioturbation structures is a promising line of research, but explicit consideration of limitations related to the scale of resolution involved and evaluation of potential diagenetic overprints is much needed. This problem is further compounded by the fact that bioturbation, through vertical mixing of sediment particles, distorts isotopic composition, an issue that has long been raised within the ichnological community, but has been analysed only recently (Hülse *et al.* 2022). These problems have made articulation of different datasets, both spatially and temporally, quite complicated. Such an integrative perspective is essential to differentiate processes that operate at ecological time (e.g. bioturbation) from those that do so at different geological time scales. These deficiencies prevent solving apparent paradoxes revealed by contrasting views from the geochemical and palaeobiological records (Dahl *et al.* 2019).

For example, framing ichnological data in a palaeoenvironmental context allows conflicting datasets on the degree of oxygenation in the Cambrian oceans to be addressed. Some geochemical studies have suggested extensive ocean anoxia during the second half of the early Cambrian (van de Velde *et al.* 2018; Liu *et al.* 2018; Dahl *et al.* 2019; Li *et al.* 2020). Notably, since bioturbation may have increased phosphorus preservation in the sediment, its increase in intensity during the first half of the early Cambrian has been deemed responsible in subsequently driving ocean anoxia (Boyle *et al.* 2014; van de Velde *et al.* 2018). It has been proposed that low oxygen conditions may have started during Cambrian Series 2 and lasted for 100 million years (van de Velde *et al.* 2018). This model assumes bioturbation depths of less than 3 cm for the whole early Palaeozoic, which is inconsistent with observational measured depths of bioturbation in rocks of this age (Mángano & Buatois 2017 and references therein). Also, since deoxygenation should have been conducive to an overall decrease in the intensity of bioturbation (i.e. generating a negative feedback), and leading to a decrease in diversity, reduction in body size, and the eventual demise of benthic communities, how this ecologic dynamic could have translated at evolutionary scale is unclear. Notably, a different picture emerges

from an ichnological standpoint, as at the time of the supposed global anoxia, a renewed increase in global ichnodiversity, a variety of styles of ecosystem engineering, and intense and deep bioturbation have been indicated in global compilations (Mángano & Buatois 2014; Buatois *et al.* 2020). Integration of ichnological and sedimentological datasets indicates that the increase in ichnological metrics is at its highest in the offshore (i.e. between fair-weather wave base and storm wave base), but the shelf (i.e. between storm wave base and the slope break) experienced a marked drop in ichnological proxies, which is more consistent with strong dysoxia to anoxia in distal settings (Buatois *et al.* 2020). Therefore, ichnological evidence supports a model of modern-style oxygen minimum zones in the outer shelf and upper slope as proposed in the study of Guillbaud *et al.* (2018), rather than an overall horizontally stratified anoxic ocean. This scenario is in sharp contrast with that of the Miaolingian and Furongian during which the decrease in most ichnological proxies is also detected in the offshore, which is consistent with the expansion of anoxia along the depositional profile (Buatois *et al.* 2020).

The deep history of ecosystem engineering has been assessed essentially in two different ways: model-driven and data-driven approaches. Both research strategies have their own merits, and scrutiny of the trace-fossil record needs to be done at some stage of the research no matter which approach is followed. In a model-driven approach, the results and predictions of the model need to be tested against the trace-fossil record as this represents hard data that cannot be overlooked. In a data-driven strategy, the resulting models should be strongly rooted in an extensive and detailed exploration of the trace-fossil record. In short, information on fossil bioturbation is extensive and keeps on growing; also, a rich conceptual and methodological toolkit is available to address substantial questions on the history of life. Ideally, detailed ichnological data needs to be integrated with other lines of evidence, including biogeochemical modelling to holistically understand the ecosystem engineering impacts of bioturbation on the Earth System.

Finally, dramatic present challenges posed by climate change are prompting evaluation of the way bioturbators may respond to the multiple stressors that are increasingly affecting terrestrial, freshwater and marine organisms. This field represents a new avenue of research in which integration of palaeobiological and modern benthic ecology data will be key. This compelling context calls for working on valuable synergies between scientific communities that have historically developed rather independently. In this regard, the study of the impact of mass extinctions on bioturbation and the resulting feedback loops (e.g. Hofmann 2016; Buatois *et al.* 2021) may provide insights into the effects of increased temperature,

acidification, and dysoxia on the benthos. This perspective from the deep past can be instrumental for delineating guidelines for predicting future impacts of bioturbation on ecosystem functioning resulting from modern climate change. Since this would require careful articulation of the different temporal scales involved, assessing bioturbation emerges as a way of providing such a link between ecological and geological times.

CONCLUSIONS

1. The significance of bioturbators as ecosystem engineers is highlighted and reviewed through a combination of spatial (i.e. local, regional and global) and temporal (i.e. short-term, intermediate and long-term) scales.
2. The work of bioturbators as ecosystem engineers at short-term and local spatial scales offers an invaluable tool to reconstruct endobenthic palaeocommunity structure and spatial heterogeneity. These studies outline the role of key bioturbators in modulating food resources and biogeochemical processes.
3. Assessing bioturbation from the perspective of ecosystem engineering at intermediate and large scales (both spatial and temporal) underscores the significance of the Cambrian Explosion in the establishment of modern-style shallow marine ecosystems; the Ordovician Radiation in the colonization of the deep sea; the continuous ecosystem impact of bioturbation during Palaeozoic terrestrialization; and the more protracted Mesozoic Marine Revolution in terms of colonization of ultra-deep tiers, the rise to prominence of regenerators, increased burrowing efficiency, and increased compartmentalization of the endobenthic ecospace.
4. The role of ecosystem engineering in deep time has been assessed essentially in two different ways: model-driven and data-driven approaches. We argue that, regardless of the approach adopted, models should be rooted empirically in the trace-fossil record, making the best possible use of the rich ichnological toolbox.
5. The study of bioturbation in the geologic record can reveal different time-scale responses of the benthic system (from community to global scale) to environmental stressors. This has potential applications at predicting expected effects on community structure and ecosystem functioning in relation to climate change.

Acknowledgements. MGM would like to thank Nick Butterfield for the invitation to give the talk at the workshop held at the Palaeontological Association meeting at Cambridge University, in which this manuscript is based. We thank the two anonymous reviewers and technical editor Sally Thomas for their useful and constructive feedback. MGM and LAB thank the

following colleagues who showed them in the field examples of Ordovician galleries: Andrei Dronov (Russia), Ursula Toom and Olle Hints (Estonia), and Linda Wickström, Michael Streng and Emma Arvestål (Sweden). Kaitlin Lindblad did the two reconstructions shown in Figures 3 and 8. This work was financially supported by the Natural Sciences and Engineering Research Council (NSERC) Discovery Grant [311727-20] to M.G. Mángano and [422931-20] to LAB. MGM acknowledges additional funding provided by the George J. McLeod Enhancement Chair in Geology. RG is funded through the BIENVENÜE program and the Interdisciplinary graduate School for the blue planet (ISblue).

Author contributions. **Conceptualization** MG Mángano (MGM); **Funding Acquisition** MGM, LA Buatois (LAB); **Investigation** MGM, LAB, NJ Minter (NJM), R Gougeon (RG); **Methodology** MGM, LAB, NJM, RG; **Writing – Original Draft Preparation** MGM, LAB; **Writing – Review & Editing** MGM, LAB, NJM, RG.

Editor. Nicholas Butterfield

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