

Bioturbation: a fresh look at Darwin's last idea

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Bioturbation refers to the biological reworking of soils and sediments, and its importance for soil processes and geomorphology was first realised by Charles Darwin, who devoted his last scientific book to the subject. Here, we review some new insights into the evolutionary and ecological role of bioturbation that would have probably amazed Darwin. In modern ecological theory, bioturbation is now recognised as an archetypal example of 'ecosystem engineering', modifying geochemical gradients, redistributing food resources, viruses, bacteria, resting stages and eggs. From an evolutionary perspective, recent investigations provide evidence that bioturbation had a key role in the evolution of metazoan life at the end of the Precambrian Era.

In the wake of Darwin

In 1837, one year after his voyage on the *Beagle*, Charles Darwin paid a visit to his maternal uncle Josiah Wedgwood, later to become his father-in-law [1]. Wedgwood took him to several fields, where 15 years earlier, the surface had been covered with lime, burnt marble and cinders. These materials were now buried at considerable depth below the surface, and his uncle believed that earthworms were the perpetrators. This seemingly 'trivial gardening matter' triggered Darwin's scientific curiosity, resulting in an interest that smouldered throughout his life (Box 1), culminating in the publication of his last scientific book *On the Formation of Vegetable Mounds through the Action of Worms with Observations on their Habits* [2]. The central topic of this book is now referred to as 'bioturbation' [3], broadly defined as all types of biological reworking of soils and sediments (see Glossary) and covering the activity of rooting plants, the impact of microbial activity, as well as the influence of burrowing animals. Here, as in Darwin's book, we focus primarily on the role of animals, from small invertebrates to large mammals (Figure 1).

Darwin thought of his bioturbation book as a 'curious little book of small importance', and referred to bioturbation as a 'subject that I have perhaps treated in foolish detail' [4]. However, a multitude of studies from a variety of disciplines, including ecology, pedology, hydrology, geomorphology, and even archaeology, now cite his book [2] as the original reference. The main reason for this is that burrowing organisms affect most, if not all, of the surface of the Earth. The exploration of the deep ocean over the past

century has shown that abyssal plains are not lifeless layered deposits, but are actively reworked by local fauna, such as brittle stars and sea cucumbers [5]. Furthermore, the way in which water-saturated sediments of oceans, lakes and rivers are reworked is remarkably similar to terrestrial soils. Both in terrestrial [6] and aquatic environments [7], animal bioturbation results from comparable activities, including burrow and mound construction, the lateral 'ploughing' of the surface (e.g. by moles or heart urchins), particle ingestion and egestion during foraging (e.g. deposit-feeding, geophagy or lithophagy), food caching and prey excavation, wallowing and trampling, and the infilling of abandoned burrow structures. In soils and sediments, these activities have a key role in the structure and functioning of the subsurface ecosystem.

Bioturbation is often researched from a biogeochemical angle, as documented in recent reviews [8,9]. Here, we focus on novel insights into the ecological and evolutionary role of bioturbation that have emerged over the past decade. Some of these ideas were already touched upon by Darwin [2], such as the notion that burrowing organisms have a proportionally large impact on their environment, which is now formalised in the concept of ecosystem engineering. Other ideas were unforeseen, such as the role that bioturbation had during the Cambrian explosion. This establishes a strong link between Darwin's bioturbation book and *On the Origin of Species* [10], a connection that would have certainly astounded the author.

An important objective of this review is to illustrate the parallel between palaeo and present-day processes, as well as the similarity between terrestrial and aquatic environments. These different facets of bioturbation are studied by separate scientific communities, which communicate their results in targeted disciplinary journals. This results in a rather slow transfer of ideas between the different research fields. Given the similarity of empirical and theoretical questions, and the complexity of the bioturbation process, interdisciplinary collaboration and efficient communication among such fields would be rewarding.

Bioturbation from an evolutionary perspective

The evolution of landscapes and seascapes

Darwin was the first to realise that small-scale reworking activities by tiny invertebrates could have dramatic consequences at far larger scales, such as in the process of landscape formation [2]. However, Darwin's concept of a biological imprint on the landscape was not picked up initially by geologists and geographers and, for more than

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Glossary

Benthos: organisms living in or on aquatic sediments. An operational classification is based on the sieve sizes that are used when sampling sediments. Macrobenthos are >1 mm, such as oysters, starfish, lobsters, sea urchins, shrimp, crabs and coral. Meiobenthos are $63\ \mu\text{m}$ – 1 mm in size, such as copepods and nematodes. Microbenthos are $<63\ \mu\text{m}$, and include unicellular organisms, such as diatoms, ciliates and bacteria.

Bio-irrigation: in a broad sense, any form of enhanced solute transport that results from sediment reworking by organisms. In a strict sense, the enhanced exchange between the pore water and the overlying water column owing to burrow flushing.

Bioturbation: in a broad sense, the biological reworking of soils and sediments by all kinds of organisms, including microbes, rooting plants and burrowing animals. In a strict sense, the enhanced dispersal of particles resulting from sediment reworking by burrowing animals.

Burrow ventilation: the active pumping of overlying water into the burrow for oxygen supply, metabolite removal or filter feeding.

Deposit feeder: animals that acquire food by swallowing large volumes of sediment, and meet their nutritional requirements from the small organic fraction of the ingested sediment (detritus and sediment-associated microbes). Although surviving on a poor food source, deposit feeders are a dominant component of the invertebrate fauna of soils (e.g. earthworms) and aquatic sediments (e.g. lugworms).

Ecosystem engineer: organisms that substantially modify the physical structure of their habitat and, thus, directly or indirectly change the availability of resources to other species.

Geophagy: eating earthy substances, such as clay, to augment a mineral-deficient diet.

Lithophagy: ingesting stones to aid digestion.

Soil and sediments: the top layer of the surface of the Earth, consisting of rock and mineral particles mixed with organic matter. In aquatic sediments, the interstitial pores are completely filled with water (saturated matrix). In terrestrial soils, a fraction of the pores is usually filled with air (unsaturated matrix).

a century, strictly physical and chemical views on Earth surface processes dominated textbooks and theories [11]. Only in recent decades has bioturbation been ‘rediscovered’ as an important factor in landscape evolution, most prominently through its influence on soil formation, erosion and hill-slope stability [12]. The production of soil through the breaking down, erosion and then transport of bedrock has been shown to be due primarily to biogenic disturbance [13]. Root growth and animal burrowing disrupt bedrock that is abiotically weathered but structurally intact; this then creates smaller particles and more surface area for weathering to act upon. Biological reworking also loosens the soil, which counteracts consolidation. This stimulates downslope creep [14] and lowers the infiltration rate of water, making the soil more prone to erosion [13,15]. Over longer timescales, this leads to a smoothing of the landscape, flattening hills and filling up valleys, resulting in an increased sediment transfer by rivers from the land to the oceans.

A similar shift from a strictly abiotic perspective to a biogeophysical and/or biogeochemical one has also occurred in our understanding of seascapes. Increasingly, small-scale bioturbation (from micrometers to meters) is considered a key factor in sediment transport, thus influencing the large-scale geomorphology (from 50 m to hundreds of kilometres) of ocean and lake sediments [16]. Benthic organisms modify the microtopography of the

Box 1. Bioturbation: Darwin’s last idea

A few weeks after his visit to Josiah Wedgwood, Darwin presented his observations in a speech ‘On the Formation of Mould’ to the Royal Geological Society [1], followed by a paper the following year [65]. In that paper, Darwin demonstrated that earthworms could displace large amounts of sediments, and advanced that this reworking activity should have a major role in soil formation. These pioneering observations on bioturbation and soil profile generation thus make Darwin one of the founding fathers of soil science [11].

Unfortunately, Darwin’s excitement did not inspire his geologist colleagues, who were expecting something more grandiose than a speech on ‘worms’. After publishing two follow-up papers [66,67], Darwin abandoned the subject. However, in December 1842, just after settling at Down House, Darwin spread a quantity of broken chalk over a nearby field ‘for the sake of observing at some future period at what depth it would become buried’. This ‘future period’ however did not arrive until some 30 years later.

In the last ten years of his life, Darwin’s fascination for earthworms was revived, and he performed several experiments on earthworm bioturbation. Revisiting the field near Down House, the chalk was now observed to be at a depth of 18 cm, a burial rate of $6\ \text{mm yr}^{-1}$. The results were synthesised in Darwin’s ‘bioturbation book’ [2], published in 1881 (Figure 1). This book described the activities of earthworms with unprecedented detail, illustrating their importance in the formation of soils humus, soil fertility and erosion–sedimentation processes.

Although Darwin himself thought of the subject as of ‘small importance’, the book became immediately popular among the general public, and effectively modified the perception of earthworms and other soil biota by society [68]. Up to then, earthworms were mainly considered as garden pests that needed eliminating from the soil [4]. Darwin changed that view, illustrating the central role of invertebrates as bioturbators, and recognizing the importance of bioturbation in the formation and functioning of soils and sediments [4,68]. Remarkably, however, the scientific community absorbed this message far more slowly [4,11], and the systematic

study of bioturbation only really began during the last part of the 20th century.

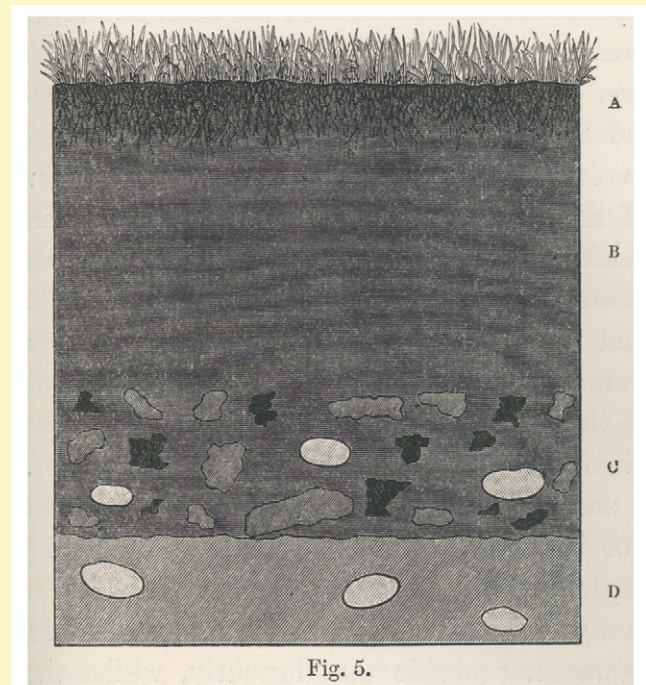


Fig. 5.

Figure 1. Reproduction of Picture 5 from Darwin’s bioturbation book [2]. This picture featured the caption ‘Section, reduced to half of the natural scale, of the vegetable mould in a field, drained and reclaimed fifteen years previously; A, turf; B, vegetable mould without any stones; C, mould with fragments of burnt marl, coal-cinders and quartz pebbles; D, subsoil of black, peaty sand with quartz pebbles.’ Reproduced with permission from [69].



Figure 1. Bioturbation results from a range of animal activities. The most eye-catching are those created by larger subterranean mammals [13], such as insectivorous moles [(a) mole track at Noordhoek beach, Cape Town] and herbivorous pocket gophers *Thomomys talpoides macrotis* (b) in prairie grasslands. In the marine environment, large-scale burrowing is also present, but less easily detectable [7]. Side-scan sonar has revealed conspicuous trenches (4-m long, by 2-m wide, by 0.4-m deep) created by grey whales in search of benthic amphipods, and long linear traces (0.4-m deep by 50-m long) generated by walrus ploughing the surface sediment in search for bivalves. In seagrass meadows, similar-sized pits and trails are created by herbivores, such as geese and dugong *Dugong dugong* (c) feeding on rhizomes. On tidal flats, smaller feeding pits (d) (up to 1-m wide and 30-cm deep) are attributed to stingrays such as the blue-spotted stingray *Taeniura lymma* (e). Small invertebrates have a small per capita impact, but are dominant from a global perspective because of their sheer abundance and ubiquity [7]; examples include ants, termites and the common earthworm *Lumbricus terrestris* (f). In the marine environment, the predominant bioturbators are deposit-feeding polychaetes and various burrowing crustaceans, such as burrowing shrimp [(g) geochemical gradients created in a laboratory observatory by the shrimp *Neotrypaea californiensis*]. Reproduced with permission from Robb Tarr (a), Richard Reading (b), Dick van Oevelen (c,e), Anthony D'Andrea (d,g), Cynthia Simms Parr (f).

ocean floor via pellet production, track formation and different types of construction, such as mounds and pits [17]. This biologically induced roughness modifies the hydrodynamics above the sediment layer, which in turn affects erosion and resuspension [8]. In addition, active sediment transport could also operate, as suspension feeders capture food particles from the water column (biodeposition) or deposit feeders eject fluidised faecal pellets into the water column (bioresuspension) [18]. Even in coastal systems, which are traditionally seen as shaped only by the physical forces of currents and waves, hydraulic engineers have recently recognised

bioturbation to be a crucial component in models of sediment dynamics [19].

In the wake of Darwin, the influence of biotic processes on topography is now an active field of investigation, and many studies stress the potential impact of small-scale interactions on the larger scale of landscapes [12] and seascapes [16]. Yet, for most landscapes and seascapes, the importance of the biological imprint compared with purely physical processes remains largely unknown. The particular role of burrowing worms, but also other biotic influences such as vegetation, remains difficult to quantify, owing to the complexity of organism–sediment interactions

Box 2. Bioturbation and the Cambrian explosion

Around 542 million years (Ma) ago, at the Proterozoic–Phanerozoic transition, there was a dramatic change in the appearance of the ocean floor. Palaeoecologists infer that, before the transition, most of the floor was covered with microbial mats (Figure 1) [58]. Such mats have a simple, one-dimensional structure, showing a regular pattern of layers, each harbouring a microbial community with a specific metabolism and with only shallow penetration of oxygen [59]. However, this well organised mat structure all but disappeared with the advent of multicellular organisms (metazoans).

The first undisputed fossil evidence for metazoan activity dates back to some 40–60 Ma before the onset of the Cambrian [60]. Trace fossil evidence suggests that these ‘Vendian biota’ or ‘Ediacara fauna’ lived in tight connection with the existing ‘pristine’ microbial mats without destroying their structure [61]. However, these early marine organisms also underwent considerable evolutionary innovation, which culminated in the relatively sudden appearance of a wide variety of animals in the fossil record. It is hypothesised that there are two important factors driving this ‘Cambrian explosion’. The first is the advent of predation [62], which promoted the development of biomineralised skeletons (bristles, spines, shells, etc.), and began an escalating ‘arms

race’ between predators and their biomineralised prey [63]. The second evolutionary factor is bioturbation, which appeared as a side effect of the skeletons induced by predation: the new armoured arrivals began to ‘bulldoze’ the ocean floor [64]. In addition to direct defence, skeletal hard parts functioned as anchoring devices or digging tools, which enabled a burrowing life style to evolve. Although the sediment now provided shelter from predators, it was also an incentive for predators to search for such prey. Burrowing also enabled the exploitation of buried organic matter as a food source, leading to the evolution of a new deposit-feeding life style.

The colonization of the deeper sediment instigated a true ‘burrowing revolution’ (also termed ‘agronomic’ [61] or ‘Cambrian substrate’ revolution [24]), as the resulting reworking of the sediment involved a dramatic change in the ecological and geochemical functioning of the ocean floor [63]. The microbial mat structure disappeared, disrupted by trilobites and other stiff-legged arthropods, intersected by complex burrow networks and covered with faeces of the newly evolved deposit-feeders [22]. Today, microbial mats only survive in extreme environments that exclude grazers and bioturbators, such as stromatolites, hypersaline lagoons and anoxic basins [59].

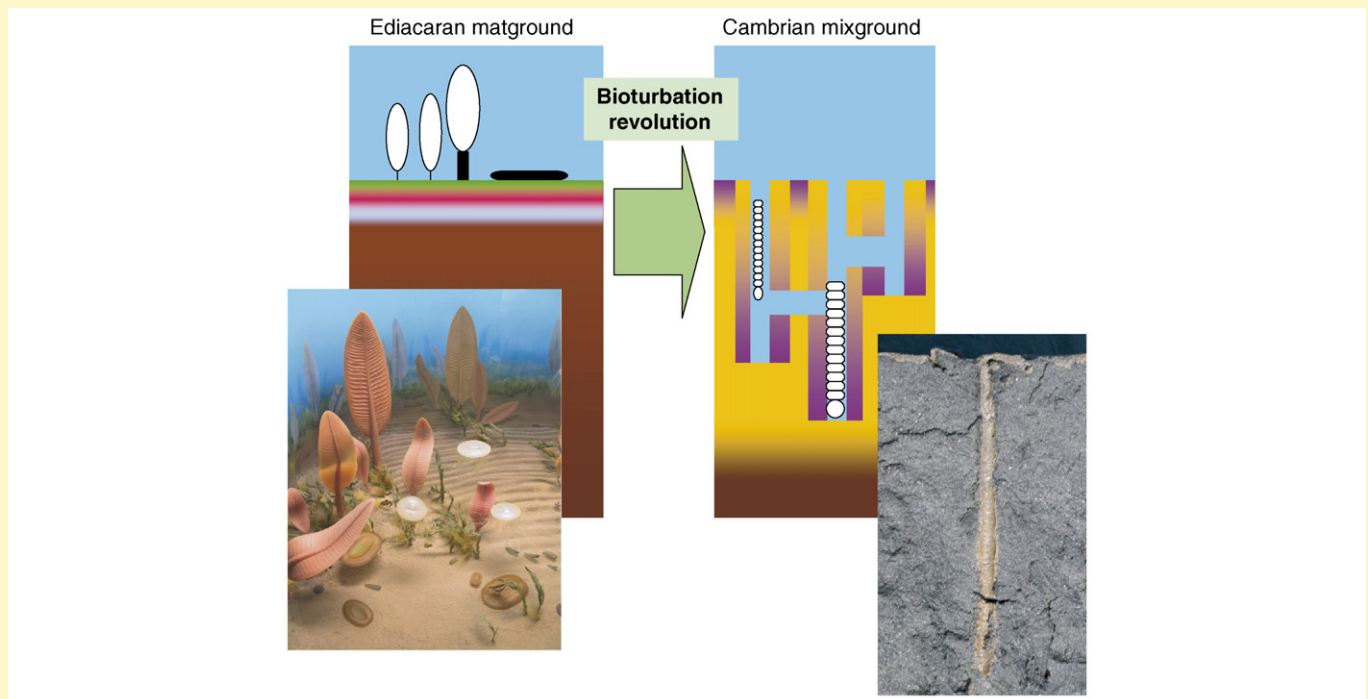


Figure 1. Transition from Ediacaran matground to Cambrian mixground during the burrowing revolution. During the Ediacaran, sediments were covered with microbial mats (a) (Vendian diorama, photo reproduced with permission from William Hargrove). After the burrowing revolution, the sediment is mixed and intersected by complex burrow networks (b). As a result of burrow flushing, oxygen is now transported deep into the sediment. The lugworm *Arenicola marina* has a light halo of oxidised sediment around its burrow as opposed to the grey background of reduced sediment (photo reproduced with permission from Oleksiy Galaktionov). Adapted with permission from [61].

at the microscale and the difficulty of extrapolating to a larger scale. Assessing how landscape evolution would proceed in the absence of life, it has been recently hypothesised that hilltops would be less smooth and rounded, whereas rivers would have coarser beds and fewer meanders [12]. To test such hypotheses, integrated landscape models that explicitly account for small-scale biotic processes in the equations that govern erosion, transport and deposition of sediment, seem promising [12,19].

Connections between bioturbation and evolution

The ‘evolution’ of landscapes or seascapes is not the only level at which bioturbation manifests. Recent studies

reveal that it also has a strong and direct impact on the evolution of modern animal forms. A fascinating point in the evolution of life is the Cambrian explosion, when a wide variety of animals appeared in the fossil record over a relatively short time [20]. This radiative explosion is now understood to have resulted from a cascade of evolutionary changes combined with biogeochemical and ecological transformations. Recent palaeo-investigations show that bioturbation had a crucial role in these ecological transformations. One intriguing speculation is that bioturbation by primitive terrestrial vegetation invoked the step-wise increase in oxygen seen during the late Precambrian, which then triggered the expansion of metazoan life at the

ocean floor [21]. The idea is that primitive land biota greatly enhanced the production of clay minerals on land (the ‘clay mineral factory’). Upon transport to the oceans, these clay particles scavenged organic matter, and increased the burial of organic carbon in sediments, which then led to enhanced oxygen levels in the atmosphere and oceans.

A second, more established connection between bioturbation and evolution comprises the ‘burrowing revolution’ (Box 2), which began in shallow marine environments, subsequently arrived in the deep sea, and finally colonised terrestrial soils [22]. This ‘revolution’ disrupted the primordial microbial mat systems, which determined the structure and functioning of the ocean floor ecosystem in Precambrian times. Owing to sediment reworking and burrow irrigation, the ocean floor entered a newly ‘mixed’ biogeochemical state (Box 2, Figure I). The thin, vertically structured microbial mats were replaced by a heterogeneous reworked layer that extends, on average, to the first 10 cm of the sediment [23]. Benthic fauna had to adapt to the newly emerging bioturbated sediment conditions, thereby fuelling the ‘Cambrian explosion’ [24]. The Cambrian fauna includes the major groups of animals known today, as well as some ‘strange’ forms that have no modern counterparts [20]. It is hypothesised that these ‘strange’ forms found in Cambrian benthic communities (such as those in the Burgess shale) were adapted to the primordial microbial mat ecosystems [25]. Thus, they might appear unusual, not because they were ‘evolutionary experiments’, but because they were adapted to an ocean floor ecosystem that no longer exists to any great extent today [24,26].

An intriguing question is whether the new subterranean lifestyle was, and still is, costly in terms of metabolism. Traditionally, burrowing has been considered more energetically expensive than other forms of locomotion, such as flying, swimming or running [27]. This inference was based on the assumption that considerable energy is required to plastically deform the muddy sediment around the burrowing animal. However, recent developments in sediment mechanics indicate that muddy sediment fractures, and that burrows extend by crack propagation, a process that requires far less energy than does plastic deformation [28]. These new insights could shed light on many ecological and evolutionary traits including infaunal lifestyle, feeding guilds and shapes of organisms. For example, deposit feeders initiate cracks in sediments and feed from the new surfaces that are produced. As an evolutionary consequence, many guilds of deposit feeders have evolved shapes (e.g. wedge-shaped clams) and tools (e.g. the proboscis of polychaet worms) to generate and utilise cracks in sediment and soils [29].

Bioturbation from an ecological perspective

Bioturbators as ecosystem engineers

As well as dam-building beavers, earthworms and other burrowing organisms have been cited as examples of ecosystem engineers [30]. The concept of ‘ecosystem engineering’ refers to a modification of the physical environment that strongly affects other organisms. All organisms affect their immediate abiotic environment in some way, but true ecosystem engineers reveal themselves when their

presence or absence has a disproportionately large impact on the ecosystem [31]. In artistic language, one could say that ecosystem engineers effectively function as authoritarian scenic designers, which not only set the stage, but also decide on the play to be performed, and select the potential players that enter the stage. Burrowing organisms meet this criterion, as exemplified by the ‘burrowing revolution’ discussed above [32]. Except where harsh conditions restrict metazoan life (e.g. strong physical disturbance, stagnant anoxic bottom water or pollution), soils and sediments are ubiquitously perforated by burrow structures in various stages of excavation, construction, maintenance and repair [9]. For structuring subsurface ecosystems, these organism–sediment interactions are considered to be at least as important as the trophic interactions classically studied by ecologists [33]. Moreover, it is now clear that the ecological consequences of bioturbation are not limited to the subsurface environment (Box 3).

In soil science, the reworked surface layer of the Earth is sometimes referred to as the biomantle [11], whereas in marine ecology, it has been termed the ‘biogenic habitat matrix’ [33]. But how does the ‘biomantle’ arise, and what is the exact role of biota in its formation? Reduced to its

Box 3. Benthic–pelagic coupling and aboveground–belowground interactions

Resting eggs and cysts of many planktonic organisms (e.g. copepods, diatoms and dinoflagellates) are found in large numbers in bottom sediments of lakes [49] and coastal sediments [50]. These dormant stages serve to secure survival through periods with harsh abiotic conditions, low food abundance or high predation risk, sometimes over periods of years–decades, making these ‘egg banks’ comparable to the seed banks of terrestrial plants [51]. Bioturbation strongly influences the distribution and dispersal of these resting stages within the sediment, either burying them upon arrival, or returning them later to the surface [52].

Recruitment from resting stages typically occurs near the sediment surface in response to some stimulus, such as temperature, light, nutrient or oxygen levels. Recent investigations reveal that bioturbation exerts significant control on the period of dormancy and, hence, on the recruitment of phytoplankton [53] and zooplankton [49]. Thus, it has a crucial role in the population dynamics of these planktonic organisms, regulating their seasonal reappearance and providing the seed stock for red tides and other harmful algal blooms. Plankton ecologists therefore tend to encompass the whole of the planktonic life cycle, including the study of survival and dispersal in the seabed, where plankters are ‘classically’ not supposed to thrive [50].

The role of bioturbation in the benthic–pelagic coupling of plankton dynamics is analogous to the above–belowground links that influence terrestrial vegetation. In the past, vegetation and soil compartments have largely been studied independently and only recently has there been a trend to assess above–belowground interactions in a more integrated view of terrestrial ecosystem functioning [54]. Burrowing activity is one such important belowground interaction, and soil invertebrates have been shown to affect plant growth in several ways: for example, earthworms influence plant competition and susceptibility to herbivores [55]; bioturbation by soil collembolans disrupts the mycorrhizal mycelial networks in grasslands, thereby influencing carbon flow through the mycorrhizosphere of the plants [56]; and nest building and foraging activities by ants influence the surrounding soil environment within and beyond the mound, with both short-term and long-term effects on soil structure, nutrient dynamics and seed banks [57]. The interactions between burrowing infauna and aboveground vegetation are therefore numerous and complex and so a more mechanistic insight is needed on the effects of bioturbation on soil microorganisms, soil invertebrates, nutrient dynamics and root systems.

barest essentials, soils and sediments constitute a porous matrix of solid particles that are coated with organic polymers, and where the gaps are filled either with an air–fluid mixture in soils, or are fully saturated with pore water in aquatic sediments. The engineering effects of burrowing fauna on this matrix are many (reviewed in [6,34] for soils and in [7,9,35] for aquatic sediments). Important biogeochemical effects are the modification of the sediment texture, the bio-irrigational transport of solutes and the dispersal of solid particles (Box 4). To understand these effects properly, one requires both a static and a dynamic perspective. Static ‘snapshots’ obtained by computerized axial tomography (CAT-scans) [36] and *in situ* sediment profile imaging [37] reveal that the physicochemical structure of the soil matrix, its so-called ‘texture’, is significantly modified by biota. Burrowing organisms create a second level of structure above the pore network, and actively determine the rheological,

mechanical and chemical properties of the porous matrix in which they live.

Apart from influencing the ‘static’ structure of the soil, there is a clear dynamic aspect to bioturbation. The chemical composition of burrow water can change drastically within minutes, while ephemeral burrow structures are created and abandoned on a timescale of hours to days. Novel imaging techniques provide a glimpse of such dynamics: planar optodes reveal clear daily cycles in burrow construction and oxygenation [38], while the use of time-lapse image analysis one show the rapid down-mixing of a pulse of fluorescent tracer particles by local fauna [37]. However, despite these advances, our current understanding of the engineering effects of burrowing organisms is still fragmentary and qualitative and, hence, a more quantitative understanding is needed. It will require not only detailed observations of how organisms behave inside sediments and soils, but also novel modeling tools that explicitly link animal behaviour with solute and particle transport [39–41].

Box 4. Biogeochemical implications of bioturbation

Modification of sediment texture

Burrowing organisms counteract compaction, glue particles together into aggregates upon egestion and tube building, segregate particles during digestion and induce spatial heterogeneity owing to particle selective feeding. These mechanisms then influence sediment properties such as porosity, permeability and, perhaps more importantly, their spatial heterogeneity [16]. These properties determine the number and diversity of micro-environments and, hence, the niches available to soil and sediment organisms.

In aquatic sediments, texture controls the diffusion of solutes, and the resistance to the flow induced by currents and waves within the sediment bed [8]. In soils, texture controls the infiltration rate of rain water, the moisture content, and the rate of diffusion of gases in and out of the soil matrix [70]. This, in turn, is crucial for the biological functioning of the soil, determining the ease with which plants extract nutrients and water, and the reagents that are available for microbial metabolism.

Bio-irrigation

When bottom dwellers create burrow networks into the anoxic zone of aquatic sediments, they are confronted with a metabolic problem. To supply oxygen and remove metabolites and toxic substances, benthic fauna actively flush their burrows with overlying water. Burrows therefore form a three-dimensional transport network that penetrates and irrigates the surrounding sediment tissue, similar to a system of veins and arteries. Strong concentration gradients emerge near the burrow wall, which enhance the diffusive exchange between the burrow and surrounding pore water [39]. In sandy sediments, burrow water is actively pumped into the sediment, thus creating flow and advective irrigation [40]. Both diffusive and advective irrigation mechanisms create biogeochemical patchiness, thus stimulating the microbial diversity within the sediment [9].

Dispersal of solid particles

A major ecological effect of bioturbation is the dispersal of various ‘solid particles’, which refers to non-living substances, such as clay, organic matter, metal oxides and adsorbed contaminants, but equally applies to particles of a biological signature, such as microbes, viruses, cysts, protists, nematodes and metazoan eggs. In recent years, some intriguing questions have been formulated regarding the evolutionary ecology [72] and the local and global biodiversity [73] of these ‘living particles’. To answer these questions, we need a proper understanding of the dispersal mechanisms of these solid particles in the subsurface environment. Recent modelling efforts have concentrated on a stochastic description of bioturbation [41], where particle displacement is regarded as a random sequence of bioturbation events (e.g. the infilling of a burrow or the passage of a crawling organism).

Biodiversity, bioturbation and ecosystem functioning

Soils and sediments are presently under pressure from various human-induced stresses, which have an impact on resident invertebrate communities. In particular, the removal of keystone bioturbators could induce large changes in the structure of the habitat as a result of reduced ecosystem engineering, with cascading impacts on local biodiversity, and soil and sediment ecosystem functioning [31]. In marine sediments, pressures on bioturbating macrofauna result from bottom-trawl fishing, pollution and eutrophication-induced anoxia [42]. In soils, resident earthworm populations have been affected by overgrazing, fertiliser application and the invasion of exotic competitors or novel predators [13,43]. Species do not need to be extinct before there is a loss of function, which could also be associated with changes in size, density or patch size [42]. Therefore, one can ask how the loss of burrowing ecosystem engineers might impact the functioning of sediment and soil [31] or, equally, how ecosystem engineers can be used to restore ecosystems and ecosystem function [44]?

A tricky problem in this regard is the selection of the ecosystem function that is studied in connection with the diversity of the macrofaunal community. Several studies have advocated the use of sediment metabolism and nutrient fluxes across the sediment–water interface as measure of ecosystem function [45–47]. The advantage here is that such fluxes are easily measured with analytical incubation techniques. However, these ecosystem functions result from a complex interplay between macrofaunal and microbial activities. For example, using the efflux of ammonium to represent ecosystem function [45], one must take into account that this flux depends inherently on four processes: the downward mixing of organic matter by macrofauna, the subsequent transformation of nitrogen compounds to ammonia by microbes, the oxidation of ammonium to nitrate by nitrifiers and, finally, the transport of the remaining ammonium to the overlying water through the active flushing of burrows by macrofauna (bio-irrigation; Box 4). Thus, owing to this complexity and

confounding factors, experimental manipulations of macrofaunal biodiversity often show idiosyncratic results [45,47].

Therefore, instead of selecting ecosystem functions that are easily quantifiable, but constitute a complex integration of microbial and macrofaunal activities, it would be logical to focus on ecosystem functions that are directly and dominantly governed by bioturbating macrofauna alone, namely physical habitat modification, bio-irrigation and the transport of solid particles (Box 4). Although the experimental quantification of these direct 'macrofaunal functions' is more challenging, such studies are slowly emerging. Using a comprehensive study of 139 benthic invertebrate species at inner Galway Bay (Ireland), Solan and co-workers [48] parameterised models that relate animal characteristics to the depth of the mixed sediment layer (mixing depth), which was measured from sediment profile images obtained by *in situ* camera systems. This parameterisation enabled them to predict how the mixing depth is affected by macrofaunal species extinction. However, because mixing depth is relatively insensitive across habitats [23], the next logical step is to link macrofaunal community characteristics with the actual rate of macrofaunal induced transport (bio-irrigation and solid-particle dispersal; Box 4).

Conclusions and future prospects

As illustrated here, there are many similarities in the reworking of marine, freshwater and terrestrial environments by burrowing animals. Strong parallels exist in the way in which small-scale bioturbation governs the evolution of the landscape [12–15] or seascape [16–19] at the large scale, the way in which burrowing invertebrates and subterranean mammals act as ecosystem engineers [34,35], and the way in which reworking activities exert control on the functioning of the water column [49–53] or vegetation above [54–57]. As marine and terrestrial ecologists develop new approaches to study these subsurface ecosystems, they will no doubt benefit from increased cross-talk. A similar synergy could be obtained by comparing past and present situations. The ecosystem engineering effects [30–33] that are studied by contemporary ecologists to understand the diversity and functioning of soil and sediment ecosystems are also those that are assessed by palaeo-ecologists when scrutinizing the role of bioturbation in the Cambrian explosion [21,22,24,58–64].

Darwin was convinced of the crucial role of subterranean biota in determining ecosystem functions, stating that 'Worms have played a more important role in the history of the world than most persons would at first suppose' [2]. One hundred twenty-five years later, a plethora of studies have now corroborated Darwin's opinion, unearthing new implications of bioturbation. Although the effects of bioturbation are clear, the actual mechanisms behind them are less established. We know that modifying earthworm density will affect plant growth and microbial diversity in soils, or that burrowing macrofauna influence the microbial diversity in marine sediments, but we are still far from a mechanistic understanding of how these causes and consequences are connected, although theoretical concepts, mathematical

models and experimental data acquisition are in early phases of development [12,16]. Many issues remain, such as the net effects of burrowing on key structural properties such as porosity and permeability [37], the importance of long-distance dispersal in subsurface particle displacement [41], and the scale and importance of lateral particle transport in marine environments [71].

Once we acquire a better understanding of the direct effects of bioturbation, we will also obtain a clearer picture of what regulates biodiversity in soils and sediment ecosystems [72,73], how burrowing engineers can be used to restore subsurface ecosystems and their functions efficiently [44], as well as how we might improve our understanding of that intriguing era when the expansion of animal life on Earth began.

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