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Trace fossils and extended organisms: a physiological perspective

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Abstract

Organism-built structures have long been useful artifacts for students of evolution and systematics, because they represent a permanent record of a set of behaviors. These structures also represent an investment of energy by an organism, and to persist in the fossil record, the energetic investment in the structure must pay off for the organisms that build it, in either improved survivorship, increased physiological efficiency or enhanced fecundity. A useful way to think about this aspect of organism-built structures is to treat them as external organs of physiology, channeling or tapping into energy sources for doing physiological work. This paper reviews briefly how burrows and nests can act as external organs of physiology at various levels of organization, and introduces the notion of organism-built structures as adaptive structures, in which feedback controls confer adaptability to organisms' external constructions, and which promote homeostasis of the organism and its local environment. Miller's concept of trace fossils as behavioral tokens reflects this aspect of animal-built structures, and may illuminate many unanswered questions concerning their origins and persistence in the fossil record.

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1. Introduction

Trace fossils commonly present two challenges to the paleontologist. On the one hand, a trace fossil indicates that an organism left an impression on its environment at some time in the past, even if the organism itself left no remains. In this case, the challenge is to connect the trace fossil to the organism that built it, whether to an organism

known from the fossil record, or to some organism whose existence can only be inferred from its traces. On the other hand, a trace fossil is also a remnant of a process, a 'frozen behavior', in which case the challenge is to reconstruct the processes that gave rise to it. Usually, this involves deriving a behavior or sequence of behaviors involved directly in its construction, such as inferring a burrowing behavior from the ways sediments are rearranged in a burrow (Bromley, 1990; Crimes, 1994).

Trace fossils can also be remnants of structures that *did* things for the organisms that built them,

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which makes them more than simply the impressions of a past existence or outcomes of past behaviors (Miller, 2002). It makes them akin to organs of an ‘extended physiology’, means of co-opting the physical environment into physiological function. In short, trace fossils can represent the remnants of ‘extended organisms’ (Turner, 2000a; Miller, 2002). This presents a third challenge for the paleontologist: recovering the past physiology the trace fossil represents. This aspect of trace fossils – ichnophysiology, if I may coin a term – is the subject of my contribution to this volume. I will develop three broad themes. First, ichnophysiology, like all types of paleophysiology, involves inference about function from structure, which requires a set of rules for how structure maps onto function. Extended physiology has a somewhat different set of mapping rules than the conventional physiology that is confined within an organism’s skin. This can make the ‘reverse engineering’ of organs of extended physiology a bit tricky. Second, extended physiology is often powered by external sources of energy, such as tides, currents, winds, gravity and light. These diverse sources of energy enable a remarkably diverse array of structures that could be organs of extended physiology. An incipient ichnophysiology should be cognizant of this diversity, and I offer a few examples from the extended physiology of modern organisms. Finally, extended physiology involves the adaptive modification of the physical environment, which blurs the distinction between the living organism and its supposedly inanimate surroundings. This raises interesting questions of scale and category, for it puts no intrinsic limit on how broadly extended physiology – whether present or past – can affect environments. This poses many challenging questions for ichnology, and I offer two: what is a trace fossil; and how is ichnology to be distinguished from the broader disciplines of paleontology, geophysiology and ecology?

2. Extended physiology and the inference of function from structure

If trace fossils can be remnants of past physiolo-

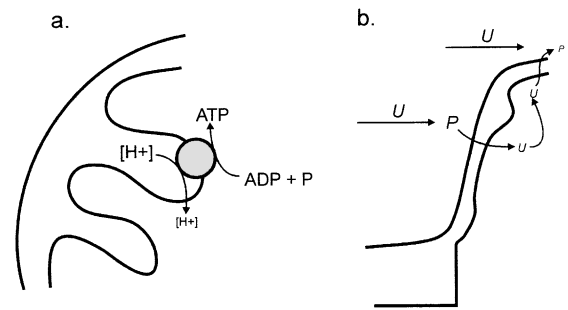


Fig. 1. Conventional and extended physiology compared. (a) Simplified scheme of phosphorylation of ADP by tapping a potential energy gradient in proton concentration ($[H^+]$) across the inner membrane of the mitochondrion. (b) Simplified scheme of a structure that converts a variation of wind speed (U) into a potential energy gradient in pressure (P), which then does work moving air through the structure.

ogy, it behooves us first to clarify what physiology is.

At root, physiology involves the adaptively controlled flow of matter, energy, or information – physiological work – across a boundary of some sort. Conventional physiology, what one might call ‘blood-and-guts’ physiology, is concerned with boundaries found within organisms, such as cell membranes, or epithelia that separate one compartment of a body from another. For example, oxidative phosphorylation of ATP in the mitochondrion is powered by the managed flow of protons down a gradient in chemical potential between the organelle’s inter-membrane space and its matrix (Fig. 1a). If the protons follow a particular pathway, determined by the complement of proteins within the mitochondrion’s inner membrane, then the work of phosphorylation can be done. Otherwise, the protons either do not flow, or do no work if they do flow, in which case their energy is dissipated as heat (Nicholls, 1982).

Physiological boundaries can exist at multiple levels, and these nest hierarchically, like Matryoshka dolls. The managed flow of protons in the mitochondrion is supported by other managed flows across the cell membrane, across exchange epithelia in the lungs or digestive tract, and so forth (Weibel et al., 1987). There is no good reason why physiology must be limited to conventional boundaries within organisms, however.

Physiological processes occur at an organism's outermost boundary, across the integumentary boundary between 'inside' and 'outside' the organism. If an organism constructs a boundary *outside* its body that adaptively manages a flow of matter, energy or information, this is as surely physiology as are similarly managed flows across, say, a cell membrane. A termite mound, for example, captures wind energy to power ventilation of its colony (Fig. 1b). The mound is simply the next larger Matryoshka doll of the termites' extended physiology (Turner, 2000a).

That biogenic structures can be organs of extended physiology is not, in itself, interesting. To assert that a termite mound is a wind-ventilated structure is akin to saying that a leg bone signifies that the animal to which it was attached could run. All would agree, I think, on the triviality of both assertions. Physiology, in whatever form it takes, is essentially a science of rates and mecha-

nisms, and it asks questions like: what is the ventilatory rate (how fast could the animal run)?; what is the cost of ventilation (what is the cost of locomotion)?; how is its function regulated (what are the stresses the bone is likely to experience)?; and so forth. If a putative ichnophysiology is to have value, it must be able to address such questions. Its ability to do so is both complicated and enriched by the peculiar rules of extended physiology.

To illustrate, let us explore the function of a U-burrow, a common architectural motif among animal burrows, both modern and fossil (Vogel, 1978; Bromley, 1990). Let us imagine an organism, like a lugworm, that uses its muscles to power ventilation through this burrow. The physiological function, ventilation, has a cost, which is roughly the energy needed to overcome the momentum loss from viscous interactions of the water with the burrow walls. The lugworm-like

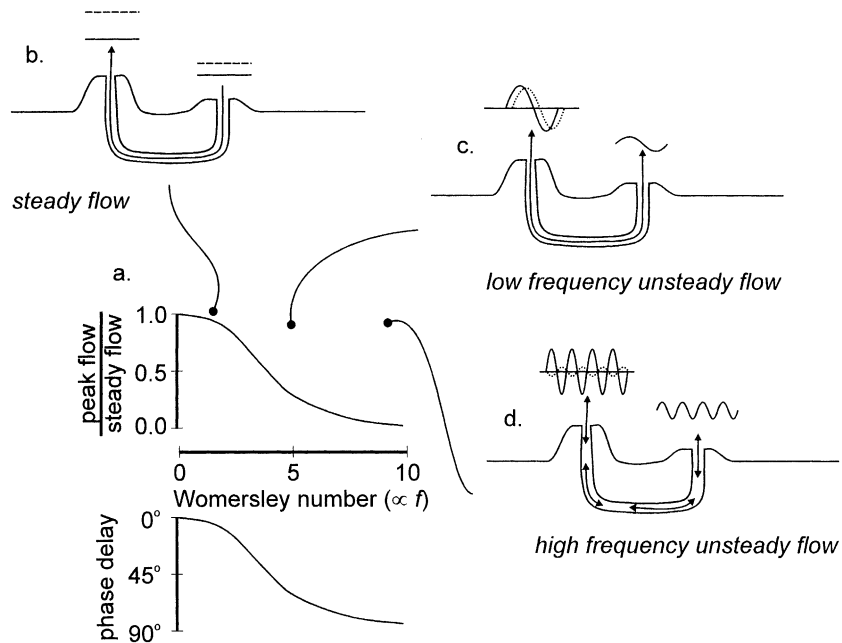


Fig. 2. Design constraints on induced ventilation of a U-burrow by external currents. (a) Currents through tubes driven by unsteady forces are determined by the frequency of change of those forces. As the frequency of the oscillatory flow increases (proportional to the Womersley number, the volume of induced flow through the burrow declines and falls progressively out of phase with the external flow. (b) When the forces driving induced flow are steady (equivalent to a frequency of 0 Hz), induced flow is unidirectional and steady. (c) At moderate frequencies of unsteady flow, induced flow through the burrow (dotted line) is attenuated only slightly compared to the driving force. (d) At high frequencies of unsteady flow, induced flow through the burrow is strongly attenuated and markedly out of phase with the external forces driving it.

creature might derive a benefit from the ventilation, let us say in enhanced productivity of the sediments surrounding the burrow. The physiological function of the burrow is therefore amenable to a simple cost–benefit analysis:

(ventilation cost) + productivity = net return

(debits are in parentheses).

The cost of running a muscle-ventilated burrow is met by an expenditure of ATP, determined by the energy required to make good the viscous losses in the flow, adjusted for the worm's efficiency at converting ATP to flow. The benefit – the enhanced productivity in the burrow's surroundings – involves the production of high quality food that can be eaten by the lugworm and converted to usable energy, also expressible as ATP. The cost–benefit analysis can therefore be expressed as an ATP budget:

$$\text{ATP}_{\text{in}} + \text{ATP}_{\text{return}} = \text{ATP}_{\text{net}}$$

which is, at root, an energy budget, and therefore constrained by conservation of energy. This makes reverse engineering of the burrow's function easier, because all these terms could, in principle, be recovered from our hypothetical fossil U-burrow. Viscous losses can be calculated from the fossil burrow's dimensions and elementary principles of fluid mechanics. Pumping efficiency can be inferred from observations of modern inhabitants of U-burrows. Enhancement of productivity could be inferred from, say, the local distribution of oxidation potential, evident as the 'halos' of oxidation that surround many fossil burrows.

Reverse engineering is only as good as the assumptions that underlie it. As always, the unstated assumptions are the riskiest. Reducing the function of the muscle-ventilated burrow to the common energy currency of ATP carries subtle implications for the structure of the 'organ' that effects the function. For example, the ATP ergonomics of organisms is tightly regulated, and this imposes a degree of regulation on all the physiological systems that support it, whether these be conventional or extended. The architecture of the muscle-ventilated U-burrow is determined largely by its impact on the organism's ATP ergonomics.

Making the burrow longer, for example, might increase the production rate of food in the sediments surrounding the burrow, but that benefit will always be limited by the increased cost of pumping that a longer burrow would require. To use the metaphor of the Matryoshka doll, the shape, even the design motif, of the outermost doll is, to some extent, determined by the nature of the innermost doll.

But what if cost of ventilation was met in some other way? Some U-burrows are 'self-ventilated' by so-called induced flow, in which the two openings of the burrow span a gradient in momentum in a surface boundary layer (Vogel, 1978, 1981). The cost of ventilation is now no longer met by ATP alone, and the architectural constraints on muscle-ventilated burrows may no longer apply to a self-ventilated burrow. Such burrows could, for example, be made longer than 'expected' for muscle-ventilated burrows, because the increased productivity in the sediments is no longer offset by an increased cost of pumping. Self-ventilation is not all free lunch, though, because it now relies on a potentially unreliable or chaotic source of energy: winds die and freshen, currents ebb and flow, flows are often turbulent, and so forth. The qualitatively different nature of the power supply now imposes its own constraints and rules on how the structure might best be built. To return to our nesting dolls metaphor, the shape and design motif of the outermost Matryoshka doll may be determined as much by the nature of the environmental source of energy as by how it interacts with those qualities in the innermost doll.

Consider, for example, induced ventilation of a U-burrow by a so-called unsteady flow, such as a tidal or wave surge. Water in the burrow would undergo periodic acceleration or deceleration as the velocity of the external flow changed with time. Each time this happens, some energy that otherwise might power ventilation now must overcome momentum: the more frequently this happens, the greater this diversion will be (Fig. 2). In short, U-burrows exposed to unsteady flows behave essentially as low pass filters. When rate of change is slow, as it might be in the ebb and flow of a tidal surge, water in the burrow is accelerated only rarely, and more of the energy in the tidal

current can power ventilation. Flow through the burrow tracks the change of external flow closely, flow is voluminous, and the burrow is ventilated uniformly. However, if external flows change quickly or frequently, more energy is diverted to changing momentum, less energy is available to power ventilation, and flows fall progressively out of phase with changes of the external flow. Volume of flow also declines: once this falls below the burrow's volume, dead spaces appear in the burrow, akin to the anatomical dead space of the lung (Fig. 2). Now, burrow length and volume may be limited to the extent of dead space, rather than any energetic limitation on cost of pumping. Just to complicate things, the burrower may invest ATP energy, as it does in muscle-powered ventilation, but use it to compensate for the shortcomings of induced ventilation. The burrow's resident might be forced, for example, to reduce dead space by pumping intermittently in synchrony with the oscillation of induced flow, an investment that can only be predicted if the nature of the driving flow is known.

Thus, the nature of the external source of power for extended physiology complicates the mapping of function onto structure on which good reverse engineering depends. This makes ichnophysiology more difficult, but not intractable. If a trace fossil is embedded in sufficient clues that betoken the energetic *milieu* in which it existed, such as evidence of turbulence, good inferences of function are still possible.

3. A potpourri of extended organisms

This limitation is offset, though, by the wealth and diversity of external sources of energy for powering physiology, which enriches the range of structures that could serve as organs of extended physiology. The best way to illustrate this diversity is among the realm of living organisms, both conventional and extended.

3.1. *Turbulence managers and the modification of landscapes*

Turbulent flow is a ubiquitous feature of natu-

ral environments, and many biogenic structures appear directed to managing it. At the simplest, we can distinguish two broad types: *turbulence enhancers*, which take a laminar or near turbulent flow, and generate turbulence, and *turbulence dampers*, which convert turbulent flows into slower or near laminar flows. In both cases, the structure is being used to manage the distribution of energy in the flow. The concept of a power spectrum is useful for understanding how.

Turbulent flow is characterized by chaotic changes in velocity, which can be partitioned into unsteady flows of various frequencies. The total energy in the flow is simply the Fourier sum of the energy in all the component frequencies. Various types of flow partition the energy differently. By shuffling energy around between various frequency components, biogenic structures can affect how the energy might be made to do work, or be dissipated as heat, or be converted to potential energy, such as pressure. A kelp forest, for example, modifies the distribution of energy in the waves passing through it (Fig. 3). Total wave energy is lower in the forest's lee, as indicated by the overall lower energy densities there. The reduction in the higher frequency components, though, is disproportionate to the reduction in the lower frequencies.

A biogenic structure can enhance turbulence by setting up a competition of sorts between the fluid's momentum (which tends to keep the fluid flowing in a straight line), and its viscosity (which tends to draw the fluid along the contour of the object in the flow). Usually this comes about by a structure forcing a fluid to abruptly change direction. A 'moderate' flow around a smooth cylinder, for example, may be laminar or nearly so, but large flutes or fins on the cylinder may generate turbulent vortices at its edges, the vortices in effect being 'torn away' by the forces which alternately impel the fluid to keep flowing in the same direction (momentum) and those that draw the fluid along the trailing edge of the fin (viscosity). Turbulence can also be enhanced by flexible structures that dynamically shape the fluid flowing past them. Fronds on kelp, for example, undulate as sea water flow past them, shedding vortices from their tips.

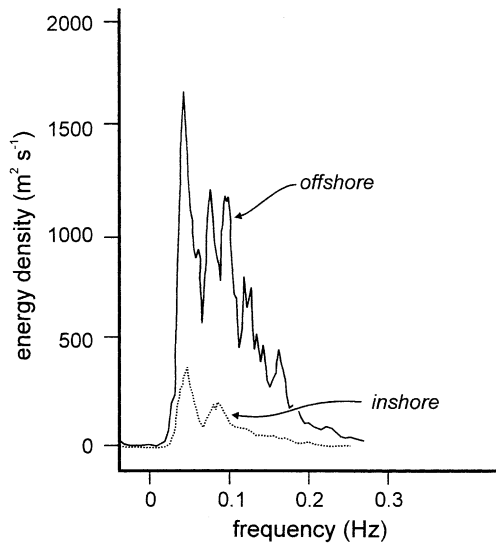


Fig. 3. An energy spectrum showing the dissipation of turbulent energy in offshore waves by a bed of the macroalga *Laminaria hyperborea*, off the rocky coast of Norway. After Mork (1996).

Like induced flow, turbulence enhancement can be used to do work that otherwise would have to be done by muscle power. Sediment feeders, for example, ordinarily dig through the sediments and separate the nutrients from the sediment burden. Simuliid larvae (Diptera) use turbulence to do the job for them (Chance and Craig, 1986). When feeding, they extend the body upward from the substratum, generating a turbulent wake. This lofts nutrient-laden sediments upwards to the larva's mouth, where they are filtered and the food items consumed. Interestingly, these larvae aggregate while feeding, which generates downstream turbulence more effectively than would be the case for solitary individuals, an interesting intersection between sociobiology and extended physiology. Such structures might leave lenses of sediment excavation in their lee that could be preserved as trace fossils.

The quintessential turbulence damper is a bushy structure, which constrains flow to open pathways between the solid elements of the structure. This tends to exclude energy in the high frequency components of a turbulent flow, leaving only energy in the low frequency components to power flow through the barrier. The energy in the ex-

cluded frequencies, meanwhile, is converted to dynamic pressure, which diverts flow around the barrier. It is noteworthy that turbulence dampers can encompass both bushes (which extrude into the boundary layer) and their topological inverse, 'bushy networks' of tunnels or spaces through which fluid can flow. Mounds of macrotermitine termites, for example, contain within them a reticulum of tunnels connecting the subterranean colony with the mound's porous surface (Fig. 4; Turner, 2000b, 2001). These damp the turbulent winds intercepted by the mound. Movements of air in tunnels just below the mound surface are oscillatory and strongly influenced by the fluctuations in turbulent winds. In tunnels near the subterranean colony, however, only long-period changes of wind speed influence the movements of air.

Turbulence dampers can also affect relief around them, which might be preserved as trace fossils. The best-known example is plants stabilizing sediments or sands in eolian and fluvial environments (Kind, 1992; Buckley, 1987). In such environments, granules kept aloft by the high frequency components of turbulent flow are re-deposited when a bush damps the energy in these high frequencies. Some structures are more effective than others: rounded bushes stabilize sedi-

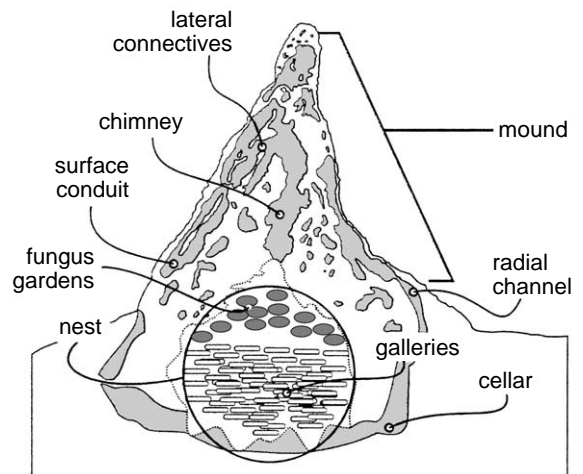


Fig. 4. Cross section of a mound of *Macrotermes michaelseni*, showing the 'bushy network' of tunnels within the mound, and locations of the colony and fungus gardens. From Turner (2001).

ments more effectively than flat bushes, for example (Buckley, 1987). The effects can extend beyond simple particle capture. Tufts of grass in steppe environments, for example, trap both organic and inorganic particles, both of which make their way into the plant. The resulting accumulation imparts considerable heterogeneity to the distribution of matter in the steppe (Kelly and Burke, 1997), which persists several months after the death of the grass clump. Foliose lichens similarly draw most of their nutrients from aerosolized particles, and their interception can concentrate minerals in the lichen to a considerable degree (Getty et al., 1999).

Turbulence enhancement and turbulence damping can have wide-scale effects on landscapes. For example, there has long been a debate over the effects of offshore kelp beds on longshore transport of sands (e.g. Bally, 1987; Kobayashi et al., 1993; Elwany et al., 1995; Andersen et al., 1996; Seymour, 1996). Offshore kelp forests are popularly thought to protect beaches, in the same way a windbreak protects soil in a field: by dissipating part of the energy in offshore waves (e.g. Fig. 3), sands and sediments are not so likely to be mobilized by turbulent waves, and so accumulate on the shore. Whether or not a kelp forest actually has this effect depends in large part on how the kelp manages the energy in the flow (Fig. 5). During a wave-driven surge through the forest, momentum will be transferred from the fluid to the kelp, some of which powers elastic deformation of the stipe. If stipe deformation is completely elastic, the presence of the kelp forest has no effect on the energy in the waves. As the crest of an offshore wave passes through, the wave does work on the stipe, but the energy is recovered when the wave's trough passes by: the stipe now does work on the wave (Fig. 6). Thus, there is no appreciable change in the distribution of wave energy near-shore to a kelp forest compared to an unforested shore (Fig. 7). Some kelp forests, though, clearly do reduce the energy in a passing wave (Fig. 3). They do so by turbulence-enhancing devices, like long fronds, with outlines and sculpturing that promote the shedding of turbulent vortices (Bally, 1987; Friedland and Denny, 1995; Hurd et al., 1997). These represent a diversion of energy in

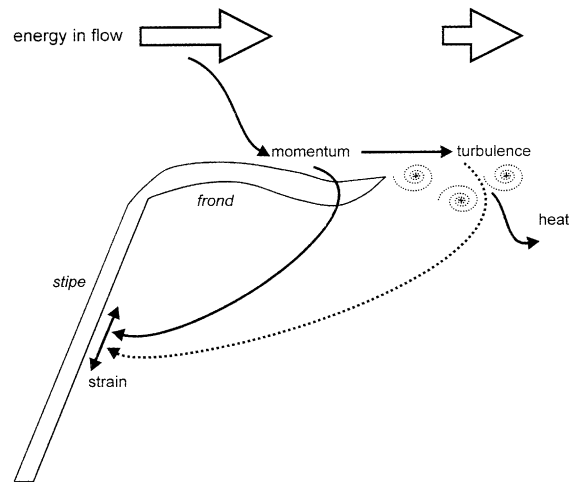


Fig. 5. Management of energy in flow by kelp. Momentum imparted to kelp can do work of stretching the stipe, increasing its risk of failure. If the frond dissipates some of this momentum as turbulent vortices, the elastic deformation of the stipe can be lessened.

the offshore flow to heat: less is therefore able to power elastic deformation of the stipe, reducing its risk of failure, and less is available to mobilize sands from the beach. This raises the interesting question: could the modification of an ancient beach qualify as a trace fossil of the ancient kelp forests offshore?

3.2. Symbiosis and organs of extended physiology

Some biogenic structures power extended physiology not only for the creatures that build them, but for other organisms as well, integrating, if you will, two ATP ergonomies. The best-known examples involve structures that exploit microbially generated redox potential gradients in sediments or soils (Rhoads and Young, 1971; Meadows and Meadows, 1991; Fenchel and Finlay, 1994; White, 1995; Ziebis et al., 1996). Generally, wet sediments contain within them a highly stratified vertical gradient in redox potential (Fig. 8). The gradient arises from a dominance of various communities of micro-organisms whose composition varies with depth. Surface sediments are dominated by obligately aerobic bacteria, protists and meiofauna, while obligately anaerobic methanogens prevail in deep sediments (Fenchel and Fin-

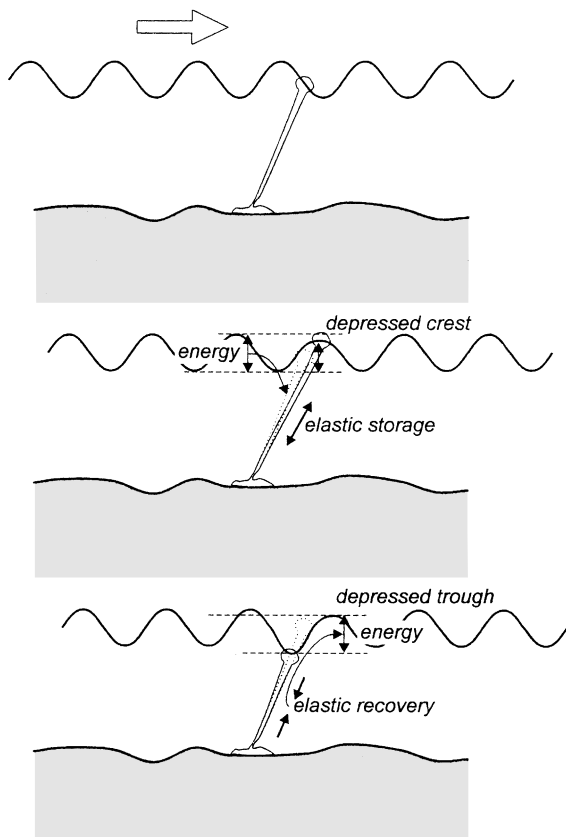


Fig. 6. Recovery of wave energy by the elastic stipe of a kelp. Details in text.

lay, 1994). In between lies an assemblage of metabolic guilds of micro-organisms, including acetogens, sulfate reducers, and nitrogen reducers, each occupying sediments corresponding to a particular band of redox potential. Metabolism in such sediments involves passing of electrons from guild to guild along the vertical gradient in redox potential, which is limited by the slow rate of diffusion of electron carriers from one guild to the next in the chain. A biogenic structure, like a lugworm burrow, that spans the redox potential gradient can, by introducing oxygen deep within the sediments, stimulate metabolism in the surrounding sediments. This can redound to the benefit of the organism building the structure as well as the organisms associated with it. Metabolism of the sediments is now controlled not by the slow diffusion of microbial metabolites, but by another

organism that controls a ventilatory flow (Andersen and Kristensen, 1991). In many burrow fossils, such activity is marked by 'halos' of discoloration or altered composition of sediments around the fossil (Bromley, 1990). The extent and shape of the halos, being a map of prevailing oxidation potential, offers a window into the extended physiology of the structure.

3.3. Gravity-powered extended physiology

Gravity is another important source of potential energy for organs of extended physiology. A remarkable example involves the feeding behavior of flamingos in tidal mudflats. A flamingo feeds by stirring up sediments with its feet, which are then processed through filters in the flamingo's beak. While feeding, the bird's head is held in one position and the body (along with the treading feet) is rotated about the head. The result is a circular trench with a hummock of filtered silt in the center. When the tide recedes, these trenches retain water throughout the low tide period (Fig.

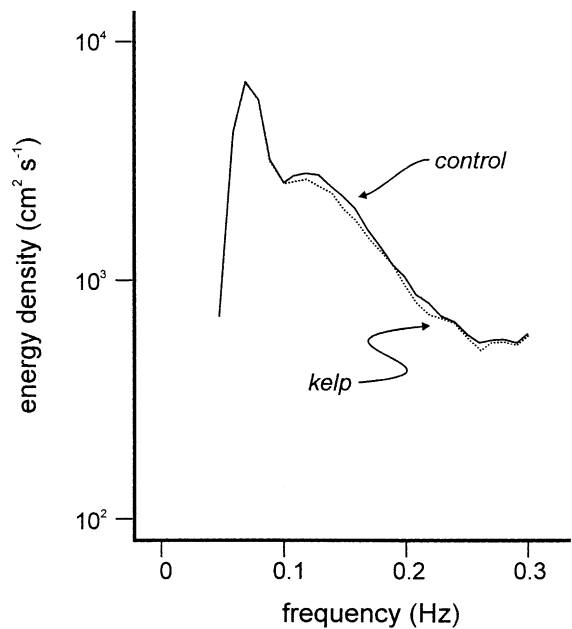


Fig. 7. An energy spectrum comparing energy in waves on-shore from a bed of the giant kelp *Macrocystis pyrifera* with energy in waves adjacent to the kelp bed. After Elwany et al. (1995).

9). The retention of water, in combination with the birds' droppings and the anoxic sediments brought to the surface by the bird's treading feet, supports a flourishing growth of bacteria, algae, protists and microinvertebrates. At high tide, flamingos return to the trenches to sort the sediments again. Thus, the feeding trenches are persistent structures, essentially flamingo-constructed ponds irrigated by tides, their productivity powered by the intrusion of the feeding trenches into anoxic sediments.

More commonly, gravity powers fluid transport by acting upon density gradients within fluids. The downward flow of water is an obvious example: even though gravity imparts a downward acceleration to both air and water, it is the water that falls because its density is greater. Natural convection is powered by more subtle variations of density, the most familiar the flows induced by local heating or altering mixtures of gases or solutes. These often support a physiological function.

Many biogenic structures interact with gravity to modify water flows through soils. Water transport through soil is a sort of competition between its downward acceleration by gravity, and its retention by matric forces within the soil's void spaces ('capillary action'). If soils are finely divid-

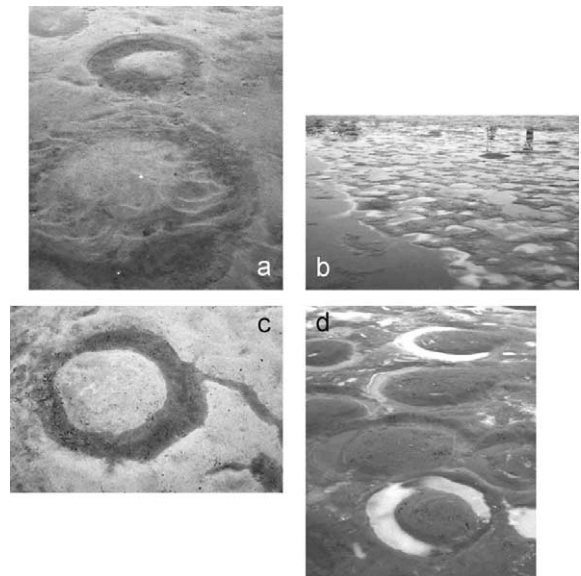


Fig. 9. Flamingo feeding trenches, located on the tidal mud flats of the Walvis Bay Lagoon in Namibia. (a) Feeding trench following receding of tide. (b) Collection of feeding trenches, showing build-up of topography and retention of water following the receding of tide. (c) Fresh feeding trench, showing exposed discolored anoxic muds. (d) Feeding trenches following an extended period of exposure, showing rich microbial growth. The true color of the water retained in the trenches is bright yellow-green. Turner (unpublished).

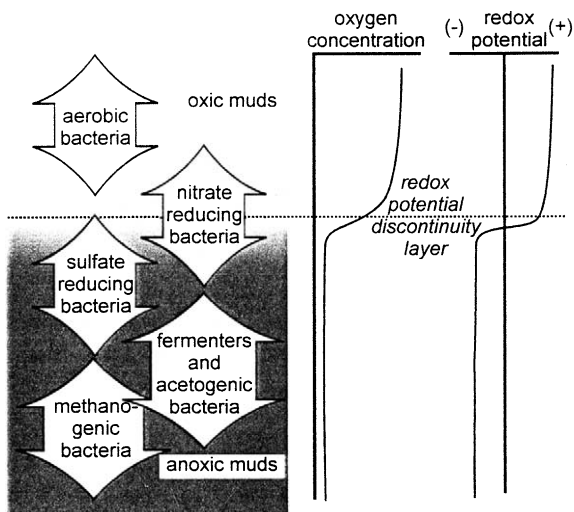


Fig. 8. Distribution of microbial communities and redox potential in a typical anaerobic sediment. From Turner (2000a).

ed, and the spaces between particles are narrow (that is, the void space is dominated by 'micropores'), matric forces predominate, so that water in rainfalls is retained in the surface layers of the soil (Childs and George, 1948; Campbell, 1977). This water usually evaporates away rapidly following a rainfall, or is so tightly held that plants or other organisms can extract it only at great metabolic expense. When soils are clumped, on the other hand, and the spaces between particles are wide (that is, the void space is dominated by 'macropores'), gravity tends to win. Rainfalls infiltrate rapidly into the soil, and are protected from loss by evaporation. The weak matric forces also mean that water is more readily available to soil organisms (Trojan and Linden, 1992).

Earthworms and other soil organisms alter the water economy of soils by retarding or reversing the course of soil weathering (Hoogerkamp et al., 1983; Joschko et al., 1992; Trojan and Linden,

1992). Soils normally tend to smaller and smaller particles as they weather, which results in an increase over time in the dominance of micropores. By their secretion of mucus-laden and calcareous fecal pellets, earthworms retard or reverse this tendency, maintaining a dominance of macropores in the soil. This results in soils with improved infiltration and aeration, and more ready availability of water to all soil organisms, both plant and animal. All can have significant effects on development and maintenance of soil horizons, as well as on transport of nutrients, minerals and oxidants within soils. All can color the interpretation of soils or tunnels as trace fossils.

Gravity-driven density gradients can interact with boundary layer gradients in momentum to exert subtle, yet broad-scale effects on transport of water and minerals in soils. A remarkable example is found among macrotermitine termites, which build large epigeous mounds above their subterranean colonies (Harris, 1956; Noirot, 1970; Ruelle et al., 1975). These mounds are physiological infrastructure for the colony, in which two sources of energy are integrated to regulate ventilation of the subterranean nest (Lüscher, 1961; Ruelle, 1964; Turner, 2000a, 2001). On the one hand, the mound intercepts wind energy in the surface boundary layer, using it to ventilate tunnels near the mound's surface. On the other hand, the tunnels deep within the mound channel a natural convection of spent air upwards from the colony, driven by metabolism-induced variations of buoyancy (Turner, 2000b, 2001). Together, the two energy sources power ventilation of the colony, which supports oxygen and carbon dioxide flux rates that are similar to those of a large ungulate herbivore (Darlington et al., 1997). Remarkably, the mound is an adaptive structure, its architecture undergoing continual modification to match ventilation rates to the respiratory demands of the colony (Korb and Linsenmair, 1998a,b; Turner, 2000b). Along with the exchange of respiratory gases, however, the mound also evaporates considerable quantities of water. Some of this water originates from the metabolism of the colony: a considerable proportion is drawn from ground water, which 'wicks' toward the colony along with its burden of dis-

solved salts, concentrating them there (Weir, 1973). Consequently, the presence of termites imparts a variegated distribution of salts in the soils, with 'blobs' of high sodium, nitrogen, and calcium interspersed with areas of relative impoverishment (Weir, 1973).

Finally, gravity-induced natural convection can have interesting effects in the deposition of sediments and their interpretation. The organic residue of surface-dwelling planktonic communities contributes substantially to marine sediments. Some marine sediments are strongly laminated, which is commonly thought to reflect episodes of high productivity in plankton communities, driven by intrusions of nutrients or oxygen through, say, upwelling events (Fig. 10a). However, rate of sediment fall is not always determined strictly by the community's productivity. Some phytoplanktonic organisms, like *Chaetoceros*, secrete organic polymers during periods of nutrient stress (commonly at the end of a plankton bloom). These aggregate individuals into larger assemblages, which sediment faster (Grimm et

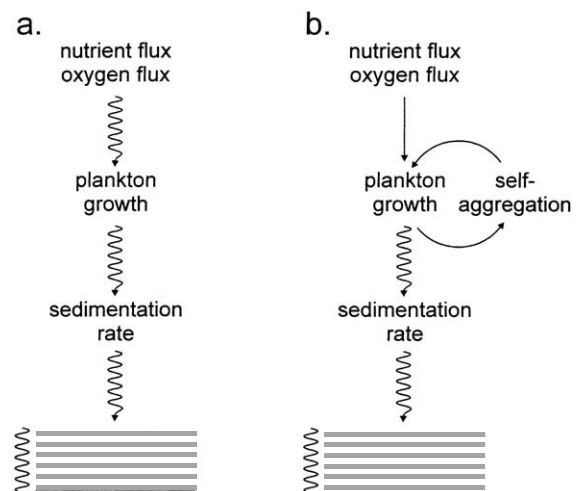


Fig. 10. Effect of self-sedimentation on patterning of lamina in sediments. (a) When sedimentation rate is simply tied to planktonic productivity, banding in sediments is a good reflection of episodic forcing of the plankton by influx of nutrients, oxygen and so forth. (b) When plankton self-aggregate and control their own rate of sedimentation, the association between banding in sediments and forcing by climate is less clear.

al., 1996, 1997; Chang et al., 1998). Laminated sediments can result from such episodes of self-aggregation rather than any forcing of productivity by external conditions (Fig. 10b).

3.4. *Species identity and organs of extended physiology*

Trace fossils are often named as species, which implies an association between particular organisms and the artifacts left by them. Consequently, a trace fossil like *Zoophycos*, which is likely the artifact of an interaction between more than one species, tends to be designated as enigmatic or problematic (Miller and D'Alberto, 2001; Miller, 2002). Trace fossils are also commonly associated with activities of individual organisms. Consequently, when that individual dies, or its kind goes extinct, it will no longer leave traces in the fossil record.

However, it is no longer clear that modification of the environment, including that which could be preserved as trace fossils, needs to be so strongly tied to individuals or species (Miller, 1996). There is a growing appreciation among ecologists that organisms and assemblages of organisms can act as 'ecosystem engineers', modifying landscapes and topographies on ecosystem-wide scales (Jones et al., 1997).

Ecosystem engineering has two salient features. First, it often involves multispecies assemblages. The mound-building termites of southern Africa, for example, are ecosystem engineers of the savanna ecosystems they inhabit, modifying landscapes, soil turnovers, carbon flux rates and mineral distributions on massive scales (Dangerfield et al., 1998). Their physiological reach is extensive because their symbiosis with fungi enables them to mobilize energy at high rates to power their 'engineering' activities (Darlington et al., 1997; Martin, 1987; Batra and Batra, 1979). Secondly, the results of ecosystem engineering are persistent, the structural modifications wrought on the environment outlasting the organisms that actually bring about the change. This, in turn, sets the selective *milieu* for succeeding generations of organisms. Such 'ecological inheritance', as it has been called, not only promotes the survival of lineages of the

original 'engineers', it also enables other lineages to compete for the engineers' self-generated 'niche' and potentially to replace them (Laland et al., 1996, 1999; Odling-Smee et al., 1996). Thus, a particular modification of the environment can persist beyond the lifetimes of individuals and even the lifetimes of species lineages, akin to Miller's (1996) conception of 'coordinated stasis'. I offer two examples.

The first involves the maintenance of reef topography through an interaction between reef-building corals, sponges and coralline algae (Wulff, 1984). The reef's topography is a balance between the rate of secretion of the calcite base, and the rate at which the base degrades, whether from wave action, erosion, predation or disease. The energy to power calcite secretion comes largely from photosynthetic symbionts within the coral. Consequently, reefs tend to grow upward, toward the light, particularly in tropical waters where dissolved nutrients are dear. If the reef breaches the surface, the resulting turbulent wave action accelerates its degradation. This is one reason why reefs tend to equilibrate around low tide levels.

Corals can maintain topography by reducing rates of reef degradation, but other organisms may play a more significant role (Wulff, 1984). Erosion of a reef generates coral rubble, small pebbles or grains of calcium carbonate (Fig. 11). These accumulate initially at low points on the reef, but wave action ensures its ultimate movement off the reef. However, sponges and coralline algae can stabilize the calcite rubble and so maintain the reef's topography. The stabilization occurs in three stages. In loose rubble, cryptic sponges penetrate through the rubble's interstices and stabilize it in a network of spongin fibers. The spongin-stabilized rubble, in turn, provides a stable substrate for erect sponges, which, in turn, set the stage for colonization by coralline algae. These incorporate the loose rubble into new calcite, which serves as a basis for new coral growth. The reef thus maintains a richer and more varied topography than it would in the absence of these colonizers of calcite rubble (Wulff, 1984). It is useful to note that maintaining the reef is not the result of associations of particular species,

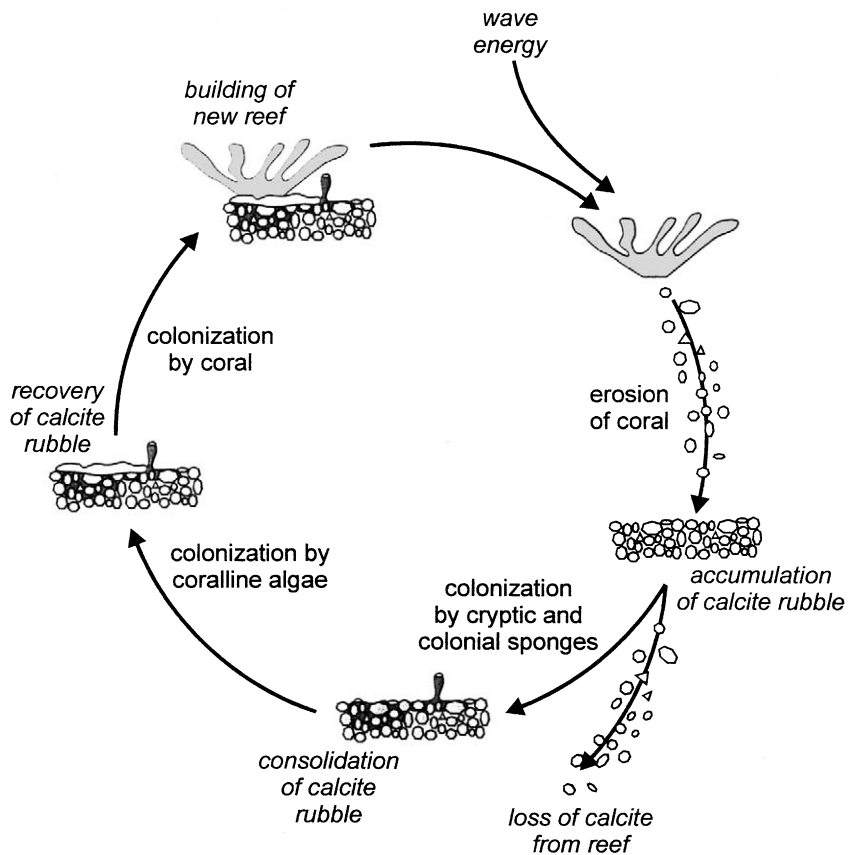


Fig. 11. Scheme of maintenance of reef topography through stabilization of calcite rubble by sponges and coralline algae (Wulff, 1984). Details in text.

but particular lifestyles: ‘weedy’ cryptic sponges, succeeded by erect sponges, succeeded by coralline algae, which sets the stage for the coral’s recolonization. If, say, one species of cryptic sponge competed effectively against another for the task of stabilizing rubble, the effect of any species turnover may be scarcely noticeable on the ‘trace’ – the reef topography.

The other example is drawn from the terrestrial realm, and involves a landform common in the winter rainfall regions of South Africa. These landforms, called *heuweltjies* (pronounced *hew-vull-key*; Afrikaans for ‘little hill’), are regularly spaced hillocks, each 20–30 m in diameter and about 2 m high (Lovegrove and Siegfried, 1989; Lovegrove, 1991). Heuweltjies are visually distinctive because they support plant communities that

differ considerably from those on surrounding soils (Fig. 12; Knight et al., 1989; Midgley and Musil, 1990; Esler and Cowling, 1995). In some instances, heuweltjies are active structures (described below), although fossil heuweltjies are also common.

A heuweltjie gets its start when a patch of ground is colonized by a harvester termite, *Microhodotermes viator*, which gathers grass, stems and other plant material from a foraging area, and returns it to the nest (Milton and Dean, 1990). The centripetal transport of this material concentrates salts, cellulose and nitrogen at the central point of the colony, as it would in any central point forager (Lovegrove, 1991). The subsequent development of the heuweltjie, however, follows from a subtle interaction between seasonal and



Fig. 12. Heuweltjies near Prince Albert, western Cape Province, South Africa. The light coloration of the heuweltjies derives from the green vegetation supported there.

geographic patterns of rainfall, soil chemistry and the adaptations of plants to these patterns. In a mediterranean climate regime like the Cape of Good Hope, winter rainfalls are reliable, albeit sparse in some localities, while summers are reliably hot and dry. Soils in the region also are well-leached and acidic (Knight et al., 1989; Midgley and Musil, 1990; Esler and Cowling, 1995). The *Microhodotermes* colony ameliorates these environmental factors in various ways. For example, the localized digestion of cellulose (which, in addition to being fixed carbon, is also fixed water) in the colony generates an ongoing input of metabolic water through the year which supplements the intermittent inputs from rainfall. Thus water is more readily available throughout the year on the heuweltjie than it is in the surrounding soils. This, in turn, establishes the conditions for the heuweltjie's subsequent development and maintenance (Fig. 13). On the heuweltjie, plant cover is denser, and the concentration of salts and nitrogen there makes them richer, which attracts a wide variety of herbivores that further disturb the soil (Milton and Dean, 1990). The termites, for their part, are attractive to other animals, like aardvark, that disturb the soil to great depths. The consequence is a eutrophication of the soils on the heuweltjie, which favors the development

of its distinctive plant communities. Water retention is aided further by generation of macropores in the soil, both by termites and by the herbivorous rodents (notably mole rats) that are attracted to the heuweltjie's plants. Over the long term, water retention in heuweltjie soils is enhanced permanently by the development of an impermeable calcareous basement layer at depths of 2–3 m (Moore and Picker, 1991), a consequence of calcite deposition from biogenic production of methane by bacteria in the termites' intestines, and the water in the moister soils. All these factors conspire to make the heuweltjie a highly persistent structure, the same spot being colonized by subsequent generations of termites. These, in turn, perpetuate the ecological conditions that help them and future generations thrive. Heuweltjies have been dated to ages of 4000 to 5000 years, with effects that have outlasted significant climate changes in the region (Moore and Picker, 1991). Like the coral reef, heuweltjies do not arise or persist because of the assemblage of any particular species. *Microhodotermes* is a common player in active heuweltjies today, but fossil heuweltjies may have been established by other termites, perhaps *Macrotermes* colonies, from a wetter time. Furthermore, the composition of the plant communities varies significantly from heuweltjie to

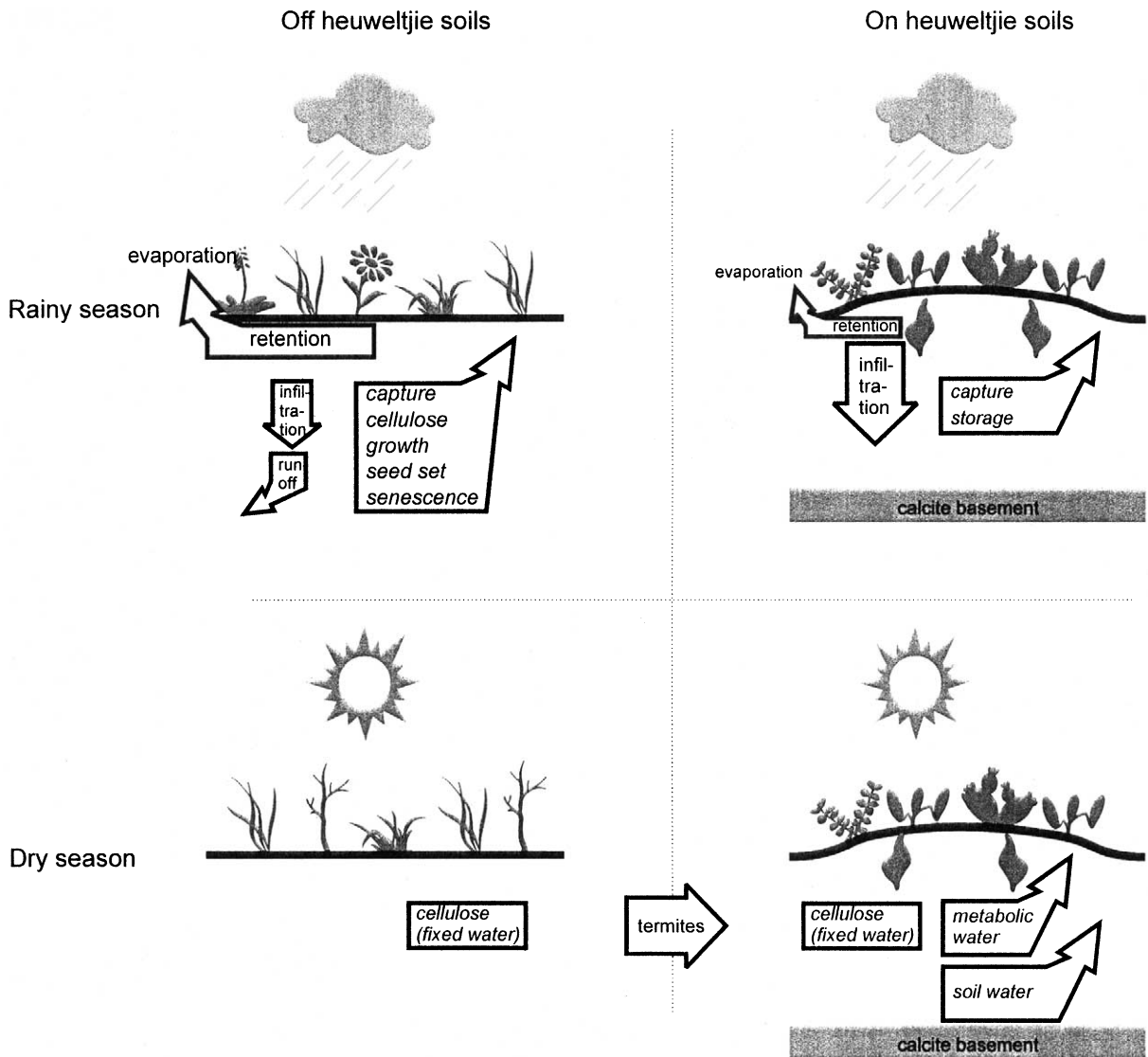


Fig. 13. Simplified schematic of water relations in a heuweltjie. Off-heuweltjie soils in the rainy season do not retain water well, have poor infiltration, and a high proportion of leaching runoff. In the dry season, off-heuweltjie soils are dry, but with water fixed in the form of cellulose. On-heuweltjie soils retain water better, have better infiltration, with leaching prevented by the formation of a calcite basement layer. On-heuweltjie soils are wetter, and water is available throughout the year supplemented by the release of fixed water through cellulose metabolism (metabolic water).

heuweltjie (Knight et al., 1989; Midgley and Musil, 1990; Esler and Cowling, 1995). In dry regions, the plant communities on heuweltjies differ from those on heuweltjies in more mesic regions. Even within a climate region, the plant communities vary substantially from heuweltjie to heuweltjie, even if the heuweltjie itself is a common fea-

ture of the extended physiology of the various assemblages.

4. What is a trace fossil?

Trace fossils obviously are the remnants of past

biological activity, but interpreting them properly seems to require an answer to the question: what type of biological activity? Certainly, trace fossils can result from an incidental encounter of organism with environment – impressions in fossilized mud, tracks, etc. Such fossils can offer penetrating glimpses into a past life. There is also no doubt that trace fossils reflect the preserved remnants of a purposeful use of the environment by an organism, whether for shelter, feeding or some other purpose. But organisms also modify environments more systematically, sometimes at massive scales, managing and driving fluxes of soil, water, nutrients, and gases through ecosystems, their reach extending even to the biosphere as a whole (Love-lock, 1991; Jones et al., 1997). Even if one does not agree with the assertion, made by some, that life is *the* most important geological force, most would probably agree that it is at least significant. And this raises the question: are fossilized remnants of this type of biological activity trace fossils?

The answer depends, of course, on just what biogenic structures represent, whether they be active or fossilized. If trace fossils represent simply the remnants of past behavior, then the answer probably would be ‘no’. The connection between longshore transport of sands, for example, and offshore kelp forests does not involve behavior, nor does it serve the interests of the kelp in any obvious or untortured way. A rearrangement of sediments in a fossil burrow, on the other hand, connects rather directly to behaviors used by an organism. Thus, one might propose that trace fossils be distinguished from other biogenic modifications of the environment by how straightforward the connection is to particular behaviors or sets of behaviors by particular organisms.

Such an approach has the virtue of focusing ichnology on a manageable subset of all the fossilized remnants of past interactions of living things with their physical environment. Lenses that focus can also obscure, however. The management of sandy beaches by kelp is a useful example: suppose kelp do derive some benefit by ensuring they face sandy beaches rather than rocky shores? There is no intrinsic reason why delimiting trace fossils as the remnants of past

behavior should necessarily obscure: Miller’s notion of trace fossils as collections of ‘behavioral tokens’, for example, which divorces the generation of trace fossils from particular organisms or even particular species, offers a broadly comprehensive and nuanced view of both the generation and interpretation of trace fossils (Miller and D’Alberto, 2001; Miller, 2002). But is it comprehensive enough to include, say, sandy beaches as trace fossils of ancient beds of kelp?

I have to confess that I am not really in a position to answer this question. As should be obvious by now, I am neither an ichnologist nor a paleontologist, but a physiologist interested in the workings of animal-built structures. However, I would just offer the following truisms, which, to a physiologist like me, are fundamental, and which lead me to wonder whether a behaviorist approach to trace fossils can be comprehensive enough. First, I offer the truism that an organism’s activities will persist only if fitness is maintained or enhanced by the activity. A second truism states that, at root, fitness and adaptation involve the mobilization of matter and energy – physiological work – to duplicate ‘winning’ variants among all the members of a lineage. Finally, there is a third truism: mobilization of matter and energy are fundamentally processes not of behavior, nor morphology, nor genetics, but of physiology.

Stating these truisms leads me to ask whether a still richer and more nuanced understanding of trace fossils might not follow from treating them not as behavioral artifacts, but as remnants of past physiology. Certainly, the case is very strong that extant organisms use the structures they build as organs of extended physiology, affecting movements of matter and energy through organisms, assemblages of organisms, ecosystems, and the biosphere (Turner, 2000a). There is no reason to believe that structures built by past organisms or their assemblages did not do the same. If so, do the artifacts of past physiology qualify as strongly as trace fossils as do artifacts of past behavior? Put another way, is the focal concentration of salts by a termite mound as much a trace fossil as, say, a fossil trackway? I think the answer is clearly ‘yes’: adopting this perspective integrates

ichnology more richly into the broader disciplines of geophysiology, geomorphology, and evolutionary biology.

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