Physical Ecosystem Engineers as Agents of Biogeochemical Heterogeneity

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Physical ecosystem engineers are organisms that physically modify the abiotic environment. They can affect biogeochemical processing by changing the availability of resources for microbes (e.g., carbon, nutrients) or by changing abiotic conditions affecting microbial process rates (e.g., soil moisture or temperature). Physical ecosystem engineers can therefore create biogeochemical heterogeneity in soils and sediments. They do so via general mechanisms influencing the flows of materials (i.e., modification of fluid dynamic properties, fluid pumping, and material transport) or the transfer of heat (i.e., modification of heat transfer properties, direct heat transfer, and convective forcing). The consequences of physical ecosystem engineering for biogeochemical processes can be predicted by considering the resources or abiotic conditions that limit or promote a reaction, and the effect of physical ecosystem engineering on these resources or abiotic conditions via the control they exert on material flows and heat transfer.

Keywords: biogeochemistry, heterogeneity, physical ecosystem engineering, sediments, soil

Locally enhanced or decreased microbially driven biogeochemical activity can often be identified in space and time. Such hot and cool spots and moments (McClain et al. 2003) are the immediate consequence of variation in resources required by microbes (energy and materials; e.g., carbon, nutrients, electron donors and acceptors) and variation in abiotic environmental conditions that control microbial process rates (reaction rates; e.g., temperature, redox potential, pH, moisture). Changes in any or all of the above can result in variation both in the types of microbial processes that occur and in their rates. But what are the ultimate environmental causes of such biogeochemical heterogeneity? Consider a patch of soil or sediment. The patch sits in a particular climatic and geomorphological setting (topography, aspect, parent material), which sets broadscale controls on microbial resources and abiotic reaction conditions (Stolp 1988). Microbes, as well as other organisms living within or above the soil or sediment, can add (dissimilate) and remove (assimilate) materials from the patch (e.g., add litter, exudates, urine, feces, oxygen, carbon dioxide, or protons; remove carbon, water, nutrients, or oxygen), also affecting resources and abiotic reaction conditions (Atlas and Bartha 1986).

However, there is also an organismal influence that does not involve assimilation or dissimilation: physical ecosystem engineering (*sensu* Jones et al. 1994, 1997). Physical ecosystem engineers are organisms that physically change the environment by their presence or activities. By affecting the physical characteristics within, on, or above a soil or sediment patch, they can change the availability of microbial resources as well as the magnitude and type of abiotic reaction controls. Countless case studies illustrate numerous ways engineering organisms can modify environments (e.g., by digging, burrowing, or damming), a variety of environments that can be modified by them (e.g., different soil and sediment types at surface and depth), and many influences of such modifications on microbial processes (e.g., denitrification, nitrification, and mineralization). But can we divine order amid this diversity? We will argue that a few underlying general principles can be used to understand the contribution of physical ecosystem engineers to the creation of biogeochemical heterogeneity.

Here we identify a series of general mechanisms by which physical ecosystem engineers can affect the occurrence or rates of biogeochemical processes. To do so, we first discuss two major types of influence on microbial resources and abiotic reaction conditions in soil or sediment patches: (1) the

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flow of materials and (2) the transmission and dissipation of heat to and from the patch. We then distinguish and exemplify the different ways in which physical ecosystem engineers can interact with these influences. We illustrate how these basic mechanisms often co-occur, but point out that they nevertheless require distinction because they do not necessarily covary. Although our examples emphasize physical effects occurring at scales ranging from millimeters to a few meters, we also briefly point out that physical ecosystem engineering can affect biogeochemical processing at finer and broader spatial scales. Last, we present a framework linking physical ecosystem engineering to biogeochemical processes, illustrating its use by example. We end with some prospects for future application of the framework.

Development of biogeochemical heterogeneity in ecosystems

The occurrence and rates of microbially driven biogeochemical reactions in a given patch of soil or sediment depend on the availability of resources required by microbes and the abiotic environmental conditions controlling reaction rates (Stolp 1988). Biogeochemical heterogeneity develops as consequence of heterogeneity in either abiotic reaction conditions, the availability of microbial resources, or both, and is largely controlled by variations in the flow of materials and the transmission and dissipation of heat to and from soil or sediments.

Variation in material flows in and out of soil and sediment patches. Both the amount of microbial resources and the magnitude of most of the abiotic variables determining reaction conditions largely depend on the fluxes of materials into and out of the patch. Fluxes of microbial resources (e.g., carbon and nutrients, oxygen, iron, sulfate) determine their local availability. Similarly, water, protons, or oxidants can flow in and out of the patch, determining abiotic reaction conditions of moisture, pH, and reduction-oxidation (redox) potential, respectively. Heterogeneity in biogeochemical processing arises when the flows transporting such materials are unevenly distributed across soil or sediment patches. These flows are driven by many different forces. For example, biogeochemical heterogeneity is often the result of variation in material transported by water (e.g., groundwater flows of nutrients; Hill et al. 2000) or the atmosphere (e.g., wind carrying nutrients; Weathers et al. 2001). In other situations, biogeochemical heterogeneity results from the active transport of abiotic materials by physical ecosystem engineers (e.g., litter burial by earthworms; Groffman et al. 2004). The transport of materials by organisms can be considered as a flux (i.e., a biotically driven flow) functionally analogous to hydrologic or atmospheric flows, albeit contingent on organismal abilities and behavior rather than the fluid dynamics of water and wind. In addition, as we will show later, organismally induced structural changes to the patches and the surrounding environment can affect hydrologically and atmospherically driven material flows.

Variation in heat transfer in and out of soil and sediment patches. The development of biogeochemical heterogeneity does not depend solely on variation in materials used in microbially driven reactions. It is well recognized that microbial activity in soils and sediments is temperature dependent (Atlas and Bartha 1986, Stolp 1988). Soil and sediment temperature are the result of heat transfer processes (direct radiation, and conduction and convection from surrounding fluids). Temperature exerts direct regulatory influences on microbial survival and metabolic rates, but also has indirect consequences for microbial activity by altering soil or sediment moisture (e.g., via evaporation or snow melting) and physical structure (e.g., via freeze–thaw cycles; Stolp 1988). Thermally induced heterogeneity in biogeochemical processing occurs via spatial unevenness in heat transfer processes. As with material flows, the structural changes caused by physical ecosystem engineers often affect these heat transfer processes. In addition, organisms can directly transfer heat to soil or sediments, and they can force convective heating or cooling by setting fluids in motion.

Contributions of physical ecosystem engineers to biogeochemical heterogeneity

Table 1 summarizes a few of the many studies showing that physical ecosystem engineers can create biogeochemical heterogeneity. While these and other examples illustrate a variety of activities and consequences, we argue that they also suggest a more restricted set of general underlying mechanisms pertaining to the material flows and heat transfer processes discussed above. Three general mechanisms change the availability of materials—modification of fluid dynamic properties of the patch, fluid pumping, and material transport (figure 1); and three general mechanisms involve changes in heat transfer processes—modification of thermal properties of the patch, convective forcing, and direct heat transfer (figure 2). After introducing these general engineering mechanisms, we exemplify how biogeochemical heterogeneity can develop from them both singly and in combination.

Modification of fluid dynamics, fluid pumping, and transport of materials. The activities of physical ecosystem engineers can alter the physical characteristics of patches and their surroundings, thereby affecting the relationship of a patch to hydrologic or atmospheric flows (figure 1, pathway 1). Structures made by engineers can affect hydraulic or atmospheric flows, resulting in amplification or reduction of the inputs and outputs of materials to soils or sediments. Such modification of the fluid dynamic properties of patches is probably the most common way in which physical ecosystem engineers affect material flows. Many organismal activities result in the formation of structural conduits for or barriers to fluid flows within, on the surface of, or above soils and sediments. Conduits within soils or sediments include animal burrows and galleries, and macropores resulting from root growth, all of which usually enhance soil infiltration, drainage, and aeration (Lee and Foster 1991, Douglas et al. 1992, Lavelle et al. 1997,

Table 1. Examples of physical ecosystem engineering activities that cause biogeochemical heterogeneity through controls on material flows, controls on heat transfer processes, or both.

Activity	Organism	Effect	General mechanism	References
Acting through controls on material flows				
Dam building	Beavers	Decreased phosphorus processing rates due to anaerobic conditions developed after retention of organic matter and increased microbial respiration	Modification of fluid dynamic properties	Klotz 1998
Generation of debris dams	Riparian trees	Increased denitrification due to trapping and retention of organic matter	Modification of fluid dynamic properties	Groffman et al. 2005
Burrowing	Fiddler crabs	Decreased sulfate reduction rates in the oxidized layer around burrows, presumably because of intense reoxidation of reduced compounds, as indicated by low pools of reduced sulfide compounds and high iron (III) content	Modification of fluid dynamic properties	Gribsholt et al. 2003
Burrowing and burrow irrigation	Polychaetes and thallasinidean shrimps	Availability of oxygen in otherwise anoxic sediments and concomitant enhancement of nitrification coupled with nitrate reduction at burrow walls via increased supply of oxic water	Modification of fluid dynamic properties; fluid pumping	Kristensen et al. 1991, Nielsen et al. 2004, Webb and Eyre 2004
Excavation and deposition of soils as surface mounds	Pocket gophers	Increased rates of nitrogen mineralization and nitrification in mounds due to soil loosening and increased air exposure	Modification of fluid dynamic properties; transport of materials	Sherrod and Seastedt 2001
Litter burial	Earthworms (exotic)	Increased microbial biomass and respiration rates due to burial of litter-derived organic carbon in recently invaded mineral soils with no previous earthworm history	Transport of materials	Groffman et al. 2004
Transport of litter to nests	Wood ants	Increased phosphorus release at nests due to transport of phosphorus-rich litter	Transport of materials	Frouz et al. 1997
Acting through controls on heat transfer processes				
Shading	Trees	Increased microbial respiration and litter decomposition under tree canopies due to increased soil moisture via reduced evaporation	Modification of heat transfer properties	Zhang and Zak 1995
Shading	Prairie grasses	Decreased soil temperature and microbial respiration due to insulation	Modification of heat transfer properties	Wan and Luo 2003
Tussock formation (accumulation of dead materials in the sedge crown)	Tundra sedge	Increased carbon and nutrient cycling in underlying soils due to soil insulation from low atmospheric temperatures	Modification of heat transfer properties	Chapin et al. 1979
Peat production	Peat mosses	Increased soil respiration due to soil insulation from low atmospheric temperatures	Modification of heat transfer properties	Petrone et al. 2001
Acting through combined controls on material flows and heat transfer processes				
Construction of litter mounds	Muskrats	Increased microbial biomass and litter decomposition within mounds due to litter exposure to aerobic conditions and insulation from external temperatures by the mound itself	Transport of materials and modification of heat transfer properties	Wainscott et al. 1990

Note: Other general mechanisms are possible for ecosystem engineering effects on biogeochemical processing (i.e., convective forcing and direct heat transfer; see text), but these mechanisms were not included in this table because of a lack of known published examples.

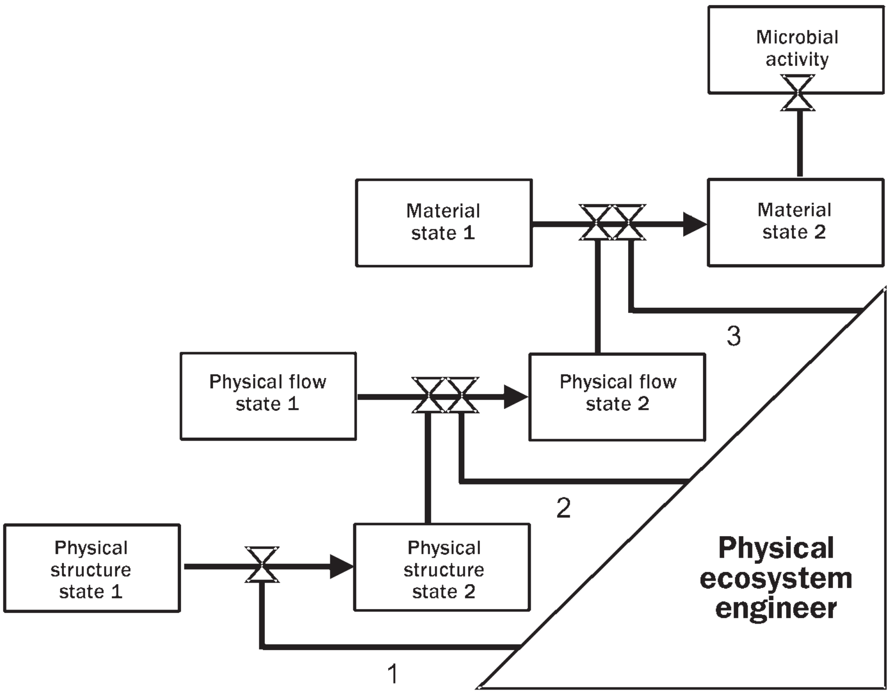

Figure 1. Creation of biogeochemical heterogeneity by physical ecosystem engineers via changes in material flows. General pathways include (1) modification of fluid dynamic properties of the patch, (2), fluid pumping, and (3) material transport. Many organisms (e.g., beavers, trees, burrowing mammals) modify the physical structure of the patch by their presence or activities (pathway 1). These changes in physical structure affect the magnitude and characteristics of fluid flows entering or leaving the patch and, in turn, the transport of materials in and out of the environment. Changes in material flows to and from the environment result in changes in resource availability or abiotic conditions (or both) that modulate the occurrence and rates of microbially mediated biogeochemical processes. In other situations, the activity of physical ecosystem engineers directly affects the magnitude and characteristics of fluid flows (fluid pumping; pathway 2) or the flow of materials in and out the patch (direct transport of materials; pathway 3). Arrows indicate state changes. Points of control or modulation are marked by intersecting triangles.

Lavelle 2002). Many plants, particularly in xeric environments, move water from deep in the soil profile to near the surface at a much faster rate than can be explained by soil capillary action alone. They do this using special roots with cells called aquaporins that allow free exchange of water. The water then becomes available to the fine roots and microbes living in the soil surface layers. This hydraulic redistribution (or hydraulic lift; Richards and Caldwell 1987) is a physical process driven by differences in soil water potential (high deep in the soil, low at the drier surface) and requiring no energy expenditure by the plant, even though the water moves through these special root conduits. Mounds built by mammals and by some ant species decrease the aggregate structure of surface materials, with concomitant increases in surface porosity, soil aeration, and infiltration, and thus effectively act as conduits on the surface (Green et al. 1999). The leaves, branches, and stems of terrestrial plants form conduits above the soil surface, conducting water to the soil surface via stem flow and drip lines (Whitford et al. 1997).

Barriers to fluid flows within soils or sediments include the formation and destruction of aggregates by infauna, and the low-permeability organic linings of invertebrate burrow walls, which decrease lateral water diffusion (Aller 1983, Bastardie et al. 2005). Animal tracks, trails, and hoofprints; termite and ant mounds with impermeable surfaces; layers of plant litter; and microbial crusts made by secretion of extracellular polymers all form barriers at the soil surface, reducing liquid and gas permeability, decreasing infiltration, and increasing runoff (Facelli and Pickett 1991, Lee and Foster 1991, Usman 1994, Lavelle et al. 1997, Eldridge et al. 2000). Barriers above the soil or sediment surface include tree and shrub canopies, which dissipate the kinetic energy of winds and result in dry deposition of nutrients to the soil surface beneath (Weathers et al. 2001), and macrophyte beds, beaver dams, and woody debris dams in streams, which reduce water flow velocity and enhance the settlement of suspended organic particles (Klotz 1998, Koetsier and McArthur 2000). In some circumstances, barriers and conduits act in combination. For example, horizontally driven fog water containing nutrients is intercepted by tree canopies and then conducted to the soil by stem flow and drip lines (Friedland et al. 1991).

The examples above illustrate the many different engineering influences on the fluid dynamic properties of soil patches via organismal creation of structures that interact with fluids. However, some physical ecosystem engineers modify the environment by direct fluid propulsion (figure 1, pathway 2). Many aquatic burrowing invertebrates circulate water within their burrows by moving their body or appendages, increasing the delivery of oxygen to deep sediment layers (Nielsen et al. 2004, Webb and Eyre 2004). Such fluid pumping is widespread in freshwater, marine, and brackish environments; it may be particularly relevant to the engineer if oxygen flow is limited; and it has well-known biogeochemical effects (e.g., in *Nereis,* discussed later; Webb and Eyre 2004). There are analogs within the plant and fungi kingdoms (e.g., evapotranspiration, root injection of oxygen or carbon dioxide into sediments, release of protons and other ions by ectomycorrhizal fungi) that have clear biogeochemical influence, but these effects generally arise from assimilatory or

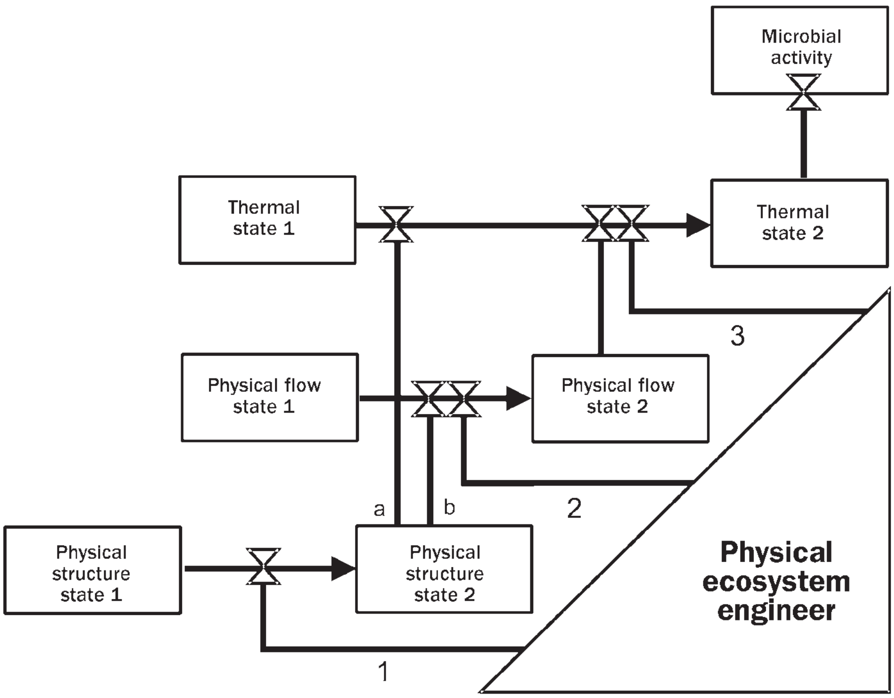

Figure 2. Creation of biogeochemical heterogeneity by physical ecosystem engineers via changes in heat transfer processes. General pathways include (1) modification of thermal properties of the patch, (2) convective forcing, and (3) direct heat transfer. Many organisms (e.g., beavers, trees, burrowing mammals) modify the physical structure of the patch by their presence or activities (pathway 1). These changes in physical structure affect heat transfer processes either by controlling conductive or radiative transfer (pathway 1a) or by causing heat convection (pathway 1b). Changes in the thermal state of the patch influence microbial survival and metabolic rates and also have knock-on consequences for microbial activity by altering soil or sediment moisture and physical structure. Note that in other cases the activity of physical ecosystem engineers directly affects the magnitude and characteristics of fluid flows that cause heat convection (convective forcing; pathway 2) or transfer metabolic heat to the patch (direct heat transfer; pathway 3). Arrows indicate state changes. Points of control or modulation are marked by intersecting triangles.

dissimilatory processes. While this uptake and release may result in knock-on chemical effects in soils and sediments (e.g., effects on soil drying, sediment redox) that can be legitimately considered to be chemical engineering (Caraco et al. 2006), they lie outside of the purview of this paper.

Physical ecosystem engineers can also increase or reduce the flows of materials to or from soil or sediment patches by actively transporting them—the exclusive province of mobile animals (figure 1, pathway 3). For example, burrowing animals usually transport sediments or soil from deep layers to the substrate surface, where they can encounter materials or reaction conditions that differ from those found at depth (Sherrod and Seastedt 2001). Similarly, a great variety of invertebrates (e.g., anecic earthworms, termites, leaf-cutting ants, land crabs, mangrove crabs) and vertebrates transport litter or plant matter, for use as food, insulation, or nesting material, into burrows and subsurface galleries where conditions for decomposition and mineralization differ from those at the substrate surface (Robertson 1986, O'Dowd and Lake 1989, Lavelle et al. 1997, Groffman et al. 2004). Such transport of materials is analogous in some ways to the pumping of fluids by physical ecosystem engineers. In both cases, the flow of materials is dependent on the occurrence of an organismal activity. However, the organismal activities involved in each case are clearly different (i.e., carrying materials versus fluid propulsion). Making the distinction is important, because the two types of activity invoke different underlying models (e.g., nesting or foraging behavior versus fluid dynamics).

Modification of heat transfer properties of soils and sediments, direct heat transfer, and convective forcing. Heat can be transferred to soils or sediments (or to any other object, for that matter) via conduction (i.e., from higher to lower kinetic energy via direct molecular collision), convection (i.e., via fluid volumetric expansion and concomitant motion along pressure gradients), and radiation (i.e., via electromagnetic transfer). Physical ecosystem engineering can affect the conductive, convective, and radiative properties of soils or sediments via modification of heat transfer properties (figure 2, pathway 1). For example, plant litter accumulation on the soil surface can act as an insulation barrier to heat conduction from the air to the soil, or vice versa (see Facelli and Pickett 1991). Similar conductive principles should apply to any engineered structure covering the surface, such as accumulations of woody debris, biological soil crusts, or beds of mollusk shells. However, in such cases the conductive insulation properties may be less important to heat balance than either (a) the reflective albedo or thermal absorption properties affecting radiative transfer or (b) the influence of such structures on convection, whereas plant litter clearly has quite marked insulation properties. While the construction of animal burrows can enhance fluid canalization, it simultaneously enhances heat convection in and out of deep soils or sediments via gravity- or flow-induced pressure gradients (Thongtham and Kristensen 2003). Crusts, vegetation, and litter cover above the soil have different albedos and different thermal absorption properties from the soil beneath (Facelli and Pickett 1991, Canham et al. 1994, Belnap et al. 2003), while mounds, pits, and a large variety of topographically engineered structures occurring on the surface alter exposure to radiation (Korb and Lisenmair 2000). Modification of the heat transfer properties of soils or sediments is probably the most common way engineers can affect soil temperature.

Physical ecosystem engineers can also induce pressure gradients that result in fluid motion and subsequent forced convection to or from sediments (figure 2, pathway 2). Examples of such convective forcing by engineers include the numerous organisms discussed in the previous section that are capable of pumping fluids. Intertidal invertebrates that irrigate their burrows with overlying warmer or cooler water should heat or cool deeper sediment layers in a relatively predictable fashion based on thermal differentials (Stanzel and Finelli 2004).

Physical ecosystem engineers can also directly transfer heat to soils via convection (figure 2, pathway 3). Ant and termite mounds usually have a higher temperature than the external environment (Farji-Brener 2000, Korb and Lisenmair 2000). Although mounds intercept more radiation than the surrounding soil, and this plays an important role in determining mound microclimate, comparison of temperatures in active versus abandoned nests has shown that the production of metabolic heat by mound inhabitants (both termite and fungus) significantly contributes to actual mound temperature (Korb and Lisenmair 2000). Heat is conducted from the organisms into the air within the nest, where it either expands and rises (free convection), moves via wind-induced ventilatory flows in the nest (forced convection; see Korb 2003), or both. Convection of heat from mound inhabitants to soil may have important consequences for microbial activity in mound soils, and may at least partially explain the often increased rates of nutrient cycling observed in mounds relative to surrounding soils (Lopez-Hernandez 2001).

Co-occurring physical ecosystem engineering mechanisms. Although we have separately considered these general mechanisms of physical ecosystem engineering effects on soils and sediments via alteration of material flow and heat transfer, it is clear that the different mechanisms can often operate in combination. Desert shrubs illustrate this point well. Higher levels of biogeochemical activity in desert soils—and of nitrogen cycling in particular—are usually found under shrub canopies compared with the less active intershrub areas (Schlesinger and Pilmanis 1998). Such "islands of fertility" are most likely the consequence of numerous co-occurring engineering mechanisms. Shrub canopies absorb and reflect solar radiation, maintaining higher soil moisture by reducing evaporation (i.e., modification of patch heat transfer properties; Pugnaire et al. 2004). Shrub canopies also periodically conduct rainwater containing dissolved nitrogen to soils via stem flow (i.e., conduit modification of patch fluid dynamic properties; Whitford et al. 1997), and intercept wind, enhancing aeolian deposition of organic matter and nutrients (i.e., barrier modification of patch fluid dynamic properties; Zaady et al. 2001). Shrubs create permeable soil mounds from intercepted dust and organic matter at their base as they grow. These mounds intercept runoff water containing nutrients and organic matter, increasing local soil moisture and nitrogen retention within shrub patches (i.e., surficial barrier and conduit modification of fluid dynamic properties; Eldridge et al. 2002). Finally, some desert shrubs transport water from depth to the surface via hydraulic lift, further contributing to local moisture enhancement (i.e., internal conduit modification of patch fluid dynamic properties; Richards and Caldwell 1987).

It is probable that all these engineering mechanisms, in addition to assimilatory–dissimilatory processes (e.g., nitrogen uptake by shrubs, shrub litter decomposition), contribute to the higher nitrogen levels and moisture necessary for greater microbial process rates in the soil beneath shrub canopies. However, the relative contribution of each of these individual mechanisms to overall process rates is likely to vary from species to species and across environmental gradients (e.g., wind, runoff, precipitation, concentration of dissolved nitrogen in rainwater). For example, the contribution of shrub mounds to moisture and nitrogen levels under shrub canopies is likely to depend on whether local abiotic environmental conditions (e.g., precipitation, soil permeability, slope) permit runoff generation. It therefore follows that the relative contributions of these underlying general mechanisms will vary from place to place and from time to time. Thus, recognizing each underlying component mechanism is important for understanding the overall effect on microbial processes, since it allows researchers to identify and predict the contingent circumstances affecting each mechanism, before the mechanisms are integrated to estimate overall effects. Such an approach is not possible as a result of focusing on net species- or guild-level effects. Therefore, the general mechanisms we have identified above for the effects of physical ecosystem engineering on material flows and temperature could serve to guide scientists as they break down overall species- or guild-level effects into the different underlying mechanisms that contribute to them in order to arrive at more general predictions that can apply across a wider variety of species and environmental conditions.

Scales of engineering effects. Although most of the examples discussed above deal with the effects of individual plants or animals that operate at spatial scales from millimeters to a few meters, it is clear that physical ecosystem engineers can affect biogeochemical processing across a broader range of spatial scales. For example, the aggregation of soil particles is usually a composite process that involves effects of individual plants and macrofauna at scales greater than a millimeter, while effects of individual meso- and microorganisms operate at smaller scales (Lavelle 2002). In addition, spatially aggregated engineers may cause collective effects at scales much larger than their individual size. Secretion of extracellular polymers by microorganisms and subsequent crust formation on the soil surface can affect patterns of water runoff at the landscape level (Eldridge et al. 2002). Similarly, the effects of vegetation on albedo can influence regional and global climate

(Bonan et al. 1992). Despite the varying scales of the effects of physical ecosystem engineers on material flows and heat transfer processes, these effects nevertheless often influence resources and abiotic conditions at microbially relevant micrometer scales.

Linking physical ecosystem engineering processes to biogeochemical consequences

The occurrence and rates of microbially mediated biogeochemical reactions in soils or sediments are a function of the availability of microbial resources and abiotic reaction conditions. Thus, if we can combine an understanding of how these resources and abiotic conditions limit or promote a particular reaction with an understanding of the effects of physical ecosystem engineers on these resources and abiotic conditions, we should be able to make useful predictions and hypotheses about the biogeochemical effects of physical ecosystem engineers.

As an example of such integration, consider a patch of muddy intertidal sediment. The high water content of the sediment means that it is anaerobic most of the time. Water saturation occurs during high tide, and the high water-holding capacity keeps the sediment close to water saturation even during low tide (Gray 1981). Aerobic conditions develop only in the top few millimeters of the sediment profile because of the limited diffusion of oxygenated tidal water and air into the water-saturated mud (Gray 1981, Malcolm and Stanley 1982). Moreover, organic matter tends to accumulate in these sediments, for two reasons. First, they often occur in gentle hydrodynamic regimes that favor settling of low-density organic matter particles (Gray 1981), and second, these organic matter inputs can often be disproportionately greater than the potential of the sediment for decomposition (Malcolm and Stanley 1982).

The combination of the above conditions has important implications for nitrogen cycling. The predominance of anaerobic conditions should increase the potential for denitrification (i.e., microbial reduction of nitrate to gaseous nitrogen, either as molecular nitrogen or as an oxide of nitrogen), because this process is carried out by anaerobic microorganisms (Sprent 1987). However, denitrification rates can be limited by the availability of nitrate. If we assume no external inputs of nitrate (e.g., land-derived loads of fertilizers) to the sediments, then the availability of nitrate will depend primarily on the rate of nitrification (i.e., microbial oxidation of ammonium to nitrite and then nitrate; Sprent 1987). Rates of nitrification, which in turn depend on ammonium availability (Sprent 1987), are unlikely to be limited by ammonium in this situation, because there is a high concentration of organic matter available for nitrogen mineralization (i.e., microbial conversion of complex organic nitrogen to inorganic forms). However, since nitrification requires oxygen, it will be restricted to the top few millimeters of oxic sediment—a relatively small proportion of the total volume of sediment. As a consequence, denitrification rates may well be limited by the availability of nitrate from nitrification (Kana et al. 1998).

Now consider what should happen if a physical ecosystem engineer that is capable of increasing the flow of oxygen to the subsurface sediments is added to a sediment patch. On the basis of the above considerations, we can predict (a) an increase in nitrification (and hence in nitrate availability) because the engineering will increase the amount of oxic environment at the sediment patch, and (b) a concomitant increase in denitrification because of the engineering-induced alleviation of nitrate limitation on denitrifying microorganisms.

In fact, this is just what happens as a consequence of burrowing and sediment irrigation by many different marine intertidal organisms. Polychaetes of the genus *Nereis,* for example, construct burrows that increase the infiltration of overlying oxygenated water into deep sediment layers (i.e., modification of the fluid dynamic properties of the patch; Webster 1992), and they also irrigate their burrows using undulating body movements (i.e., fluid pumping; Evans 1971). The combination of burrowing and irrigation substantially extends the oxic sediment–water interface into deep, otherwise anoxic sediments (Kristensen et al. 1991, Nielsen et al. 2004). The sediments located a few millimeters from the burrow walls are a zone with high rates of nitrification (Kristensen et al. 1991, Nielsen et al. 2004), and there is substantial evidence that this enhancement of nitrification rates near burrow walls is a consequence of enhanced microbial nitrification due to increased oxygen availability (Nielsen et al. 2004). This enhancement of nitrification in the oxic sediments surrounding burrow walls results in a net increase in nitrate reduction and denitrification in the anaerobic, nitrate-containing layers adjacent to the oxic zone, and an overall enhancement of these processes at the patch and tidal-flat scale where *Nereis* occurs (Kristensen et al. 1991, Nielsen et al. 2004).

We can further illustrate this approach with respect to the effects of physical ecosystem engineers on heat transfer. From the examples given earlier, it is clear that physical ecosystem engineering can increase or decrease soil and sediment temperature to varying degrees. Nevertheless, engineer-induced changes in temperature should be relatively predictable, given knowledge of the thermal environment and an understanding of how the engineering activities affect heat transfer properties, directly transfer heat, or cause convective forcing. The consequences of these changes in temperature for microbial activity should be predictable on the basis of microbial thermal requirements. Such thermal requirements are encompassed by cardinal temperatures for minimum tolerable, optimum, and maximum tolerable temperatures (the latter is the temperature at which protein denaturation occurs; Stolp 1988). Any temperature change (either increase or decrease) toward the optimum will increase microbial activity, while changes in the opposite direction will decrease activity. The shape of the function between microbial activity and temperature can be described by the optimum and maximum tolerable temperatures; these are usually close together, but distal from the minimum tolerable temperatures (i.e., as temperature increases beyond the optimum, microbial activity rapidly drops to zero; Stolp 1988). This asymmetric functional response suggests that a physical ecosystem engineer that affects temperature within the range of the optimal and maximum tolerable temperatures will have a larger effect than an engineer that affects temperature in the same magnitude and direction toward the optimum, but within the range of the minimum tolerable and optimal temperatures.

The above examples illustrate how knowledge about resources and abiotic conditions that limit or promote biogeochemical reaction rates, combined with an understanding of the effects of physical ecosystem engineers on such resources or abiotic conditions, can provide a potentially powerful framework for predicting the effects of physical ecosystem engineers on biogeochemical processes. Given a focus on a particular biogeochemical reaction (or a series of related biogeochemical reactions) of interest, we suggest three general features that need to be known in order to use the framework to predict the effects of physical ecosystem engineers on biogeochemical processes. First, the resource levels and abiotic conditions necessary for the microbial reactions to occur at particular rates need to be identified. Second, the resources and abiotic reaction conditions of the abiotic environment of interest need to be known. Third, the ways in which the physical ecosystem engineer can affect these resources or abiotic reaction conditions via its influence on material flows or heat transfer need to be invoked. In principle, the framework could be made operational for other existing case studies, and then evaluated by judging its success in prediction across these cases. However, with the notable exception of the *Nereis* studies above, there are few extant studies that provide sufficient detail on the underlying mechanistic pathways from engineering activity to biogeochemical effect to allow a rigorous evaluation of the framework. By no means do we consider the current framework a finished product. Rather, we consider it a potentially useful tool motivating the development of testable working models and hypotheses about the mechanisms that mediate the effects of physical ecosystem engineers on biogeochemical processes.

Summary and prospects

Biogeochemistry and ecosystem science have traditionally emphasized the roles of organisms as assimilatory–dissimilatory compartments in element cycling. However, there are countless examples showing that the nontrophic physical ecosystem engineering activities of organisms are ubiquitous and can often have a large influence on the spatial and temporal distribution and rates of microbial processes. An increased appreciation of such engineering influences has important ramifications. For example, it can help researchers identify species and microenvironments that are of major importance to overall ecosystem functioning (Nielsen et al. 2004, Webb and Eyre 2004). Similarly, practices of ecosystem management and restoration could well be enhanced by understanding spatial and temporal variation in biogeochemical processing resulting from physical ecosystem engineers.

Overall, we hope we have shown that the concept of physical ecosystem engineering emerges as useful for recognizing a series of nonassimilatory, nondissimilatory effects of organisms on the physical properties of the abiotic environment that have knock-on consequences for biogeochemical processing. Although the details of such activities and the pathways of biogeochemical effect are complex and quite variable, the ecosystem engineering perspective allowed us to (a) identify a more limited set of general mechanisms affecting material flows and heat transfer in soil or sediment patches, and (b) create a framework linking these effects on microbial resources and abiotic reaction conditions with their consequences for biogeochemical processes.

While such advances in understanding might be construed by some as being rather limited, we argue that they can substantially inform further development in this field of study, for two reasons. First, the general mechanisms of physical ecosystem engineering on material flows and heat transfer provide an internally coherent scheme for organizing a plethora of diverse examples into a more general conceptual body of knowledge. Given this, it should be possible to develop a comparative understanding of the contributions of different physical ecosystem engineers to biogeochemical heterogeneity in the same or different environments. Second, while the predictive examples we gave were qualitative, the general mechanisms are potentially amenable to formalization into quantitative models. The principles of fluid dynamics or thermodynamics apply directly to all of the general engineering mechanisms, except for the transport of nonfluid materials by organisms, which is purely a biologically driven process. This implies that magnitudes, rates, and frequencies of fluid material or heat delivery to soil or sediment patches could be estimated by linking metabolic or behavioral models of ecosystem engineers with basic physical principles. The connection to biogeochemical process rates can then be quantitatively addressed by combining estimates of the magnitude of engineer effects with quantitative relationships between microbial reaction rate maxima and thresholds and abiotic resources and conditions. In our view, these two possibilities represent interesting avenues for future research.

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