Biodiversity and Ecosystem Processes in Freshwater Sediments
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Source: *Ambio*, Vol. 26, No. 8 (Dec., 1997), pp. 571-577
Published by: Springer on behalf of Royal Swedish Academy of Sciences
Stable URL: http://www.jstor.org/stable/4314671
Accessed: 06/06/2014 15:49

Article Margaret A. Palmer et al.

Biodiversity and Ecosystem Processes in Freshwater Sediments

All freshwater eventually passes through or over sedimentary habitats on the way to oceanic or atmospheric domains. These zones of freshwater sediments contain an enormous variety of species that produce and process organic carbon. Some species perform specific functions such as fixing or recycling nitrogen. Others break down contaminants or mix sediments so as to alter the rates of ecosystem processes. Approximately 175 000 species have already been described and yet still, new species continue to be discovered. Their diversity and distributions range greatly along gradients of depth, dissolved oxygen, latitude, and altitude in wetlands, lakes, rivers, and groundwaters. Deep, isolated habitats contain unique, endemic species especially among those organisms with limited dispersal ability. Competent scientists must be trained in many parts of the globe to accelerate studies of this species-rich biota and essential ecosystem relationships.

INTRODUCTION

Freshwater is an essential resource for life, its flow is used as an energy source, it is a habitat for much of Earth's biodiversity, and it influences Earth's climate (1). Freshwater links the land and the oceans via groundwaters and riverine flow and is especially important in the cycling of elements such as nitrogen and phosphorus. Freshwater habitats respond to climate change and cultural impacts from a wide range of human activities. The most obvious responses to such perturbations are in surface waters, but changes that occur in subsurface habitats—where most of the world's freshwater resides—are of major significance. These "unseen" habitats harbor biota that are central to fundamental ecological processes at local and global scales. Degradation of freshwater sediments will limit the availability and quality of surface water, disrupt global biogeochemical cycles, destroy habitats for many unique species, and alter our climate and the flux of gases globally. Because the biota associated with sediments mediate biogeochemical transformations that ensure proper vitality or functioning of freshwater ecosystems, protecting this biota is essential.

The major subsurface habitats in freshwater include the sediments of running waters (rivers and streams), of lentic bodies (ponds and lakes), of groundwater zones, and of ecotonal waterbodies where two aquatic habitats meet (e.g., hyporheic zones, wetlands, marshes and estuaries). Subsurface habitats can be viewed as habitats along a physical continuum: high flow/large particle environments→ low-flow/fine sediments (Table 1). Sediment size and water-flow rates play important roles in determining the biological diversity and abundance of bottom-dwelling (benthic) organisms in freshwater even for those biota that spend some of their life cycle in the water column or on land. Ecotonal waterbodies may be the most important subsurface habitats and can be viewed as transfer control zones because they often determine the physical and biological state of the adjacent terrestrial and aquatic ecosystems. As suggested in Figure 1 and Table 1 in the article by Freckman et al. (2), transfer

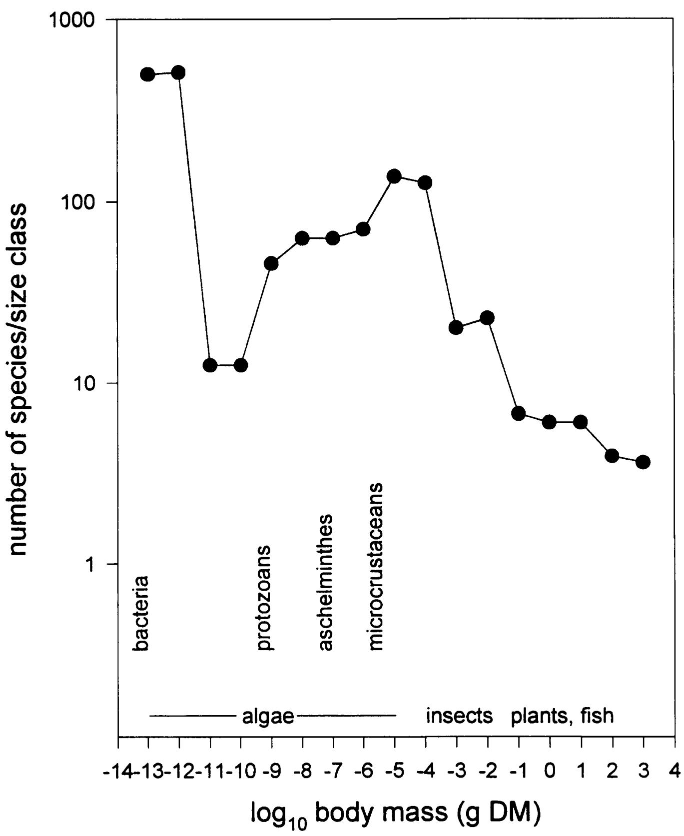

Figure 1. Approximate, hypothesized distribution of species richness versus body size in a "typical" freshwater sediment ecosystem. Plotted are the number of species in a size class, each of which spans an order of magnitude of body mass. Note that both axes are logarithmically scaled. Based on moderate local richness from Table 3 and data on body sizes from various sources.

Table 1. Major freshwater subsurface habitats. Two factors that have a major impact on biodiversity in freshwater sediments are water flow and bottom substrate particle size. Flow and substrata vary predictably from the surficial sediments in running water habitats to the deep sediments below running waters (hyporheic zones) and porous groundwaters to bodies of slow-moving or stagnant waters such as lakes.

Habitats	Water flow	Substrate size
Near-surface sediments of running waters (streams, rivers)	Fast and temporally variable	Large
Deep sediments below running waters (hyporheic zone) Alluvial (porous) groundwaters	Slow	Fine to moderate
Lakes, ponds, wetlands	Very slow	Fine

control zones may regulate the movement and fate of materials between land and waters.

BIODIVERSITY IN FRESHWATER SEDIMENTS

About 175 000 species of organisms associated with freshwater sediments have been described (Table 2), but the true number of species certainly is much higher than this. Efforts to document biodiversity in freshwater sediments have been hampered by a lack of species-level baseline information for many groups. New species are being found every year in most taxa. Research on the archaea, bacteria, fungi, protozoans and small, soft-bodied invertebrates has been especially inadequate (1, 3). The number of species in most of these taxa can scarcely be estimated (4, 5) and global estimates of microbial biodiversity remain highly controversial (6, 7). For example, researchers estimate that there are hundreds of thousands of aquatic nematodes and only a few percent of these have been described; microcrustacean and especially, rotifer species diversity are poorly known for freshwater sediments but are estimated to include 1000s of undescribed species (8). The most speciose taxa in the freshwater sediments are the invertebrates (especially dipteran insects, nematodes and crustaceans).

Most freshwater sediment species are small and are concentrated in the upper sediment layers (Figs 1, 2). Several factors affect local species richness. For many taxa, the number of species changes from the sediment surface to deep sediments to underground waters (Table 3; Fig. 2). Availability of light restricts plants and photosynthetic bacteria (photoautotrophs) and thus they are scarce or absent in some groundwaters and in the sediments of deep lakes and shaded streams. Oxygen levels may also influence species richness. Because most eukaryotes are obligate aerobes, the number of species (although not necessarily the number of individuals) is low in anoxic waters. Finally, because of long-term stability and geographic isolation, some freshwater sediments support large numbers of endemic species.

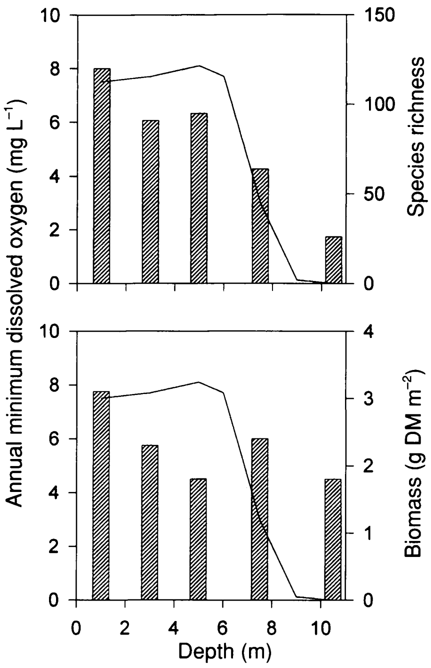

Figure 2. Typical relative species richness (upper panel, bars) and biomass (lower panel, bars) of freshwater sediment invertebrates versus water depth based on data from Mirror Lake, New Hampshire, USA. (59). The solid line in each panel shows the annual minimum dissolved oxygen concentration near the sediment-water interface.

Such endemism is particularly well known among poorly dispersing taxa such as mollusks and crustaceans, but even groups traditionally thought of as cosmopolitan (e.g., chydorid Cladocera) may turn out upon careful taxonomic examination to contain many local endemics (9). Examples of regions supporting high numbers of endemics include the Balkans, Lake Baikal, Lake Titicaca, Lake Tanganyika, rivers of southeastern North America, and groundwaters (10, 11).

Throughout the world, freshwater organisms are threatened biota (12). Pollution, hydrologic modifications, and landscape alterations have eliminated many local populations of freshwater organisms (13). Humans drastically reduce freshwater benthic biodiversity not only by pollution and misuse of drainage basins, but also by accidental and, in some cases, intentional introductions of non-native species. These species often displace native species in the short term through direct or indirect competition or by spread of diseases. However, these invasive species may not be well adapted for long-term, highly variable environmental conditions and in most cases, we do not know if they contribute to ecosystem processes as effectively as native species over the long run. Once these non-natives encounter the extremes of natural variation in the environment, they may die off, but the native species may not be able to recover because they have been lost from the ecosystem.

Certain species or certain functional groups (= species with similar ecological roles) of freshwater sediment biota play pivotal roles in ecological processes that are central to healthy freshwater ecosystems. The ability for freshwater ecosystems to persist in a healthy state, despite species loss, is low in freshwater habitats that are dominated by functional groups that typically have only a few species and in freshwater habitats with few species due to extreme conditions. The latter includes anoxic waters and groundwaters with

Table 2. Species richness of the freshwater sediment biota. Numbers are very approximate and derived from many sources (47–55) and for many habitat types (e.g., wetlands, lake and stream bottoms, groundwaters).

Taxon	Number of species described globally	Probable number of global species	Range of local species richness
Bacteria	> 10 000	unknown	> 1000
Algae	14 000	> 20 000	0–1000
Fungi	600	1000–10 000	0 - 300
Protozoa	< 10 000	10 000–20 000	20–800
Plants	1000	unknown	0–100
Invertebrates	70 000	> 100 000	10–1000
Aschelminthes	4000	> 10 000	5–500
Annelida	1000	> 1500	2–50
Mollusca	4000	5000	0–50
Acari	5000	> 7500	0–100
Crustacea	8000	> 10 000	5–300
Insecta	45 000	> 50 000	0–500
Others	1400	> 2000	0–100

Table 3. Typical local species richness of the freshwater sediment biota by habitat type. Numbers are very approximate and derived from published (56–59) and unpublished sources.

Taxon	Lakes	Streams	Groundwaters
Bacteria	> 1000	> 1000	> 100
Algae	100–1000	0–1000	0
Fungi	50–150	150–300	0–10
Protozoa	200–800	100–500	0–20
Plants	0–100	0–100	0
Invertebrates	200–1000	200–1000	10–150
Aschelminthes	0–500	0–500	2–20
Annelida	10–50	10–50	2–20
Mollusca	0–30	0–50	0–10
Acari	10–100	10–100	0–10
Crustacea	25–150	25–150	5–60
Insecta	50–500	50–500	0–10
Others	10–50	10–50	1–20

very low water flow. Examples of species-poor functional groups in freshwater sediments include benthic invertebrates that tear apart decaying leaves and other organic matter while feeding (the shredders) and sediment fauna that stir up and displace sediment while they move or feed (the bioturbators).

THE ROLE OF SEDIMENT BIOTA IN FRESHWATER ECOSYSTEM PROCESSES

Ecosystem functioning refers to ecological processes such as the breakdown of organic material and the recycling of nutrients. Healthy freshwater sediments are those in which ecological processes continue unimpeded to ensure that water is clean and plentiful and that organic matter is not lost or accumulating in excess. The benthic fauna play a key role in these processes (Table 4). The most important ecological processes in freshwater sediments are decomposition of organic matter, the uptake and transfer of materials, and production by green plants and certain bacteria. All three of these processes are influenced directly or indirectly by sediment biota and by the availability of oxygen, which in turn has a huge influence on the sediment biota. Indeed, the maintenance of aerobic conditions in surface sediments is a basis for high diversity for aquatic biota in most freshwater sediments. If organic inputs to the sediments are not in balance with the decomposition capacity, the functioning and biodiversity of subsurface ecosystems will be radically altered, which may result in degradation of the groundwaters associated with those sediments and, eventually, the adjacent surface waters.

Decomposition of Organic Matter

This process releases dissolved organic carbon, inorganic carbon, and nutrients to the environment, with the result that production by photosynthetic organisms, bacteria, and larger organisms can proceed, and that wastes and dead organic matter do not build up. The sources of dead organic matter (detritus) for decomposition are mainly algae, macrophytes (emergent aquatic plants such as cattails, floating plants such as water hyacinths, and submerged plants such as pond weeds and macroalgae), and terrestrially produced leaf and woody litter, or dissolved organics from groundwater and runoff. Once deposited within freshwaters, the large pieces of organic matter (particulate organic matter) (see also Fig. 2, ref. 2) can enter into a storage mode through deposition on the surface of sediments in areas with very little water flow or through burial within the sediments. The amount of particulate organic matter remaining in storage varies dramatically by system; streams with relatively rapid flows may have little particulate organic matter in storage, whereas large portions of the carbon may remain as particles in the sediments of profundal lakes. Particulate organic matter can move from the storage mode into a processing mode through both direct (e.g., ingestion) and indirect (e.g., mechanical breakdown) effects.

Direct biotic effects: The direct processing mode includes use of organic matter by (i) aerobic respirers (bacteria, algae, fungi, invertebrates); and (ii) anaerobic respirers and fermenters (bacteria, protozoa, and some invertebrates). Dissolved organic matter released during organic matter processing and decomposition includes a range of compounds, many of which can be used by bacteria. Because many sediment-dwelling organisms ingest these bacteria, dissolved organic matter is introduced into the food web via the "microbial loop." Microbial-loop processes have not received much study in sedimentary environments, largely due to methodological difficulties, but our concept of the microbial-loop in general is very well developed. Microbial loop processes may have great significance in sediments, especially in shallow freshwater sediments where fungi are abundant and act to further enhance microbial loop trophic transfers.

Thus, direct processing of organic matter by sediment biota facilitates recycling of nutrients via the microbial loop and prevents build-up of dead organic matter. Since species richness of eukaryotic anaerobic processors is relatively limited and species redundancy is likely to be much lower compared to assemblages of aerobic species (14), loss of the former species may lead to environmental degradation, especially in freshwater sediment ecosystems that tend to be dominated by anaerobic processes (e.g., some wetlands).

Indirect biotic effects: The indirect processing mode includes physical-chemical alteration of substrata by fauna that *(i)* fragment or shredd particulate organic matter while not ingesting it (e.g., by stoneflies, decapods, caddisflies); *(ii)* re-package sediments through formation of fecal pellets (e.g., by many types and sizes of invertebrates); *(iii)* produce organically-rich "slime layers" (biofilms) composed of complex sugars, proteins and other organic substances (e.g., by bacteria, algae, and fungi); and *(iv)* regulate organic-matter processing via invertebrate ingestion of bacteria and fungi (15–17). Through their feeding, many types of micro- and macro-fauna influence the abundance and reproductive rates of bacteria and fungi. Because the latter are the primary decomposers in freshwater sediments, the feeding by larger fauna often acts to stimulate rates of decomposition (18). Of these four indirect effects, particulate organic matter fragmentation (shredding) is probably the most sensitive to species loss because there are relatively few species of sediment biota in freshwater ecosystems that perform this function.

Transfer of Materials: Fluids and Particles

Movement of water, mineral, and organic particles through freshwater sediments determines the efficiency, mode, and rate of

Table 4. The role of freshwater sediment organisms in key ecological processes.

Biotic Group	Functional Role
Bacteria	Chemical or photosynthetic production (autotrophy), consumption of organic matter (heterotrophy), biofilm production (effects sediment stabilization, sediment clogging, deposition of sulphurz), breakdown of organic matter and release of nutrients, nitrification, denitrification, dinitrogen fixation, oxidation and reduction of sulfur and iron compounds, degradation of organic components, precipitation of heavy metals.
Algae	Photosynthetic production of new plant material (autotrophy), biofilm development (sediment stabilization, etc.), sediment formation
Fungi	Decomposition of organic matter, biofilm production (sediment stabilization, organic matter storage), mediative activities (symbiotic).
Protozoa	Regulation of decomposition (bacterial grazing), of fungal and bacterial population densities. (*)
Plants	Photosynthetic production of new plant material and oxygenation of sediments, baffle water flow, sediment trapping, and sediment stabilization.
Invertebrates	
Aschelminthes	Regulation of decomposition via microbial grazing, bioturbation
Annelida	Regulation of decomposition and autotrophy through grazing (*), bioturbation, sediment formation, repackaging of sediment
Mollusca	Bioturbation, sediment formation, repackaging of sediments.
Acari	Regulation of decomposition through grazing.(*)
Crustacea	Bioturbation, regulation of decomposition through grazing (*), physical breakup of detritus (shredding), repackaging of sediments.
Insecta	Bioturbation, regulation of decomposition through grazing (*), physical breakup of detritus (shredding), repackaging of sediments.

* All organisms from protozoa through insects that influence decomposition indirectly due to microbial grazing, probably, also act to regulate fungal and bacterial population densities.

biogeochemical processes. The influence of sediment biota on the movement of these materials varies, but the movement of all materials through aquatic ecosystems is influenced greatly by bioturbating species that mix surface and deep sediment (19). No empirical work has been completed to determine levels of functional redundancy within this important group; however, based on the few number of species we could identify belonging to this category, we hypothesize that functional redundancy may be very low and thus, species loss of bioturbators could be detrimental to sustaining ecosystem services.

Biotic effects on water movement: Freshwater animals may increase or decrease the rate at which water flows through sediments. Bioturbators can move significant amounts of sediment causing an increase in the rate of water movement through sediments. Other freshwater sediment species exude biofilms that coat sediment particles, litter, and act as a rich microhabitat for sediment fauna and flora in aquatic ecosystems. Biofilm producers, e.g., bacteria, algae, bind sediments and decrease water flow through the substrate (19). Experiments in slow sand filters of waterworks and in alluvial aquifers showed that protozoans, tubificid oligochaetes, nematodes, and chironomids may enhance sediment permeability, both directly by grazing on microbial biofilms, and indirectly by sediment ingestion, pelletization, and bioturbation (20, 21). Large animals that are not living within the sediments may also have a tremendous effect on freshwater sediment ecosystems. The activities of organisms that modify the landscape in a significant way, such as beavers and hippos, often alter the sedimentary habitats in major ways that create areas of standing water and compacted sediments (22). While we often do not think of "landscape modifiers" such as beavers, as sediment biota, they are indeed closely tied to the sediments for their feeding and other activities and can have huge impacts on ecological processes in freshwater sediments. Similarly, macrophytes, woody debris, and riparian vegetation can reduce flow rates significantly, thereby altering sediment processes and biota.

We hypothesize that there is sufficient species redundancy among the biofilm producers (6, 7) that loss of a single species may have little impact on water movement. In contrast, we suggest there is limited redundancy for the bioturbators, macrophytes, and landscape modifiers so that loss of single species may have major impacts on the flow of water and its quality (19, 22).

Biotic effects on the movement of sediments: To some extent, most of the species that affect water movement also affect the movement of sediments. Some freshwater animals bind sediments, e.g., by producing biofilms or dense mats of tubes or filaments, thereby reducing sediment transport and loss from the system. Conversely, other sediment animals may enhance suspension and transport of sediments, e.g., due to burrowing or feeding activities. Bioturbators probably enhance suspension while the roots and emergent stems of aquatic plants and the activities of filter feeders bind sediment and enhance deposition thereby increasing water clarity (23). This binding, in combination with reduced flow velocity in the presence of macrophytes or woody debris, also acts to decrease movement of sediments. Some species actually produce new sediments, e.g., biogenic sediments such as calcareous deposits (24). We hypothesize that species loss of bioturbators, macrophytes, or biogenic sediment-builders would radically alter movement of sediments in freshwater ecosystems because functional redundancy in these groups is low, i.e., there are few species performing the functions.

Biotic effects on movement of gases: Freshwater organisms influence the transfer of gases from sediments directly to the atmosphere or indirectly through floating and emergent plants. They may increase sediment oxygen concentrations while facilitating the flow of nitrogen gas, methane, and carbon dioxide from sediments to the atmosphere. Biota influencing the movement of dissolved gases from surface waters to sediments include plants, bioturbators and tube-builders (19, 25). We suggest that the two groups for which biodiversity loss may have a great effect on the movement of these gases are macrophytes and bioturbators.

Biotic effects on the movement of contaminants: Freshwater biota may increase or decrease the concentration of waterborne contaminants through bio-accumulation processes and/or the direct degradation of toxic materials. Certain species of bacteria are capable of reducing nutrient loads in agricultural areas, e.g., denitrifying bacteria reduce levels of nitrate in groundwater, and of breaking down contaminants such as petroleum products (hydrocarbon-degrading bacteria). Macroinvertebrates may act to remove contaminants from the water through a variety of processes such as filter feeding or the binding of contaminants to their body surface (26). Bioturbators, however, may actually increase the movement of contaminants from the deeper sediments into the overlying water and thus we cannot assume that sediments are a final sink for contaminants. Bacteria are probably the most critical to contaminant removal from freshwater sediments, but to date there is no information on the biodiversity or functional redundancy of the relevant microbes.

Plant Productivity: Autotrophic Processes

The synthesis of organic matter by primary production is a key process in freshwater sediments. Shallow, well-lighted sediments may be autotrophic, but deep sediments that receive no sunlight are heterotrophic. Rates of primary production are variable across freshwater ecosystems, ranging from low in poorly-lit habitats such as groundwaters and turbid or heavily-shaded streams to among the highest rates on the planet in some tropical freshwater wetlands. As is the case with respiration, primary production may proceed by different metabolic pathways. Here, we recognize two main pathways; photoautotrophy and chemolithotrophy.

Photoautotrophy: Photoautotrophs use light as a source of energy and either water or reduced sulfur as an electron donor. Familiar and important photoautotrophs in benthic freshwater habitats include algae, macrophytes, photosynthetic bacteria, and cyanobacteria (27). These organisms can form complex and highly productive communities, as in the case of benthic algae and bacteria in streams that produce biofilms and the microalgal/cyanobacterial assemblages in nearshore lake zones (16). Production by any of these groups may be substantial depending on the ecosystem. In some stratified freshwater lakes, most of the photoautotrophic production may come from micro-algae living symbiotically inside Protozoa (6). Photosynthetic bacteria are restricted to illuminated, anoxic sites with a source of electron donors from minerals such as sulfur.

Chemolithotrophy: The other broad class of primary producers, the chemolithotrophs, uses the oxidation of inorganic chemical species, e.g., ammonium, ferrous iron, hydrogen, sulfide, methane, as a source of energy and carbon dioxide as a source of carbon. Examples include the methanotrophic bacterium *Methylosinus trichosporium* and the nitrifying bacteria *Nitrosomonas europea* and *Nitrobacter winogradskyi* (28–30). Among the many groups of chemolithotrophs, methanotrophic bacteria are particularly important in freshwater sediment environments. Methanogenesis accounts for approximately 50–80% of carbon mineralization in freshwater sediments (31). However, only a fraction of this methane reaches the atmosphere; 50–100% of methane diffusing into oxic sediments is oxidized to CO_2 by methanotrophic bacteria (32).

Although the physiologies of most chemolithotrophs impose strict requirements for both molecular oxygen and a suitable reduced chemical species, consequently restricting their distributions to locations having both resources, such locations are common. Oxic/anoxic interface zones can be found near the sediment-water interface, and at the boundaries of oxic and anoxic water masses in thermally stratified lakes with seasonally anoxic layers of unmixed waters. Chemolithotrophic oxidation of reduced chemicals can account for a major fraction of oxygen consumption at such oxic/anoxic interfaces, often dominating oxygen consumption at freshwater lake sediment/water interfaces (30). Major increases in nutrient fluxes into freshwaters (e.g., due to agricultural activities) can shift the main pathway of productivity in freshwater sediments from oxygen-producing macrophytes and green algae in well-oxidized sediments to other types of algae and bacteria that create anoxic sediments and use minerals as a source of their energy. This elimination of oxygen from the sediment results in increased production of greenhouse gases such as carbon dioxide and methane.

In most cases, many species contribute to autotrophy, so there may be functional redundancy in the sense that a change in the species composition of the autotrophs may not cause a marked change in rates of primary production (33). Nonetheless, a shift in species composition of the autotrophs may result in important changes in the quality of the organic matter that is produced, with consequent changes throughout the food web (34). Major shifts in sediment chemistry from oxidized muds to anoxic muds will greatly alter the rates of productivity and result in higher production of greenhouse gases.

RESPONSE TO DISTURBANCE

Disturbances to freshwater ecosystems are caused by physical, chemical, biological and cultural forces and vary greatly in terms of their magnitude, predictability, and temporal nature. "Pulse disturbances" are short-term events, "press disturbances" are long-term and constant in strength (35), and "ramps" are long-term and steadily changing disturbances (36). Note that, particularly in running-water systems, a disturbance includes the failure for an event to take place; for example, land-use changes or dams that remove predictable seasonal floods can have large effects on the sediment biota, through physical redistribution and resource alteration.

Arrival of non-native organisms (including pathogens) constitutes a form of disturbance that is increasing in frequency in freshwater ecosystems (37). Introduced fish may not only deplete or outcompete native fish populations but, in a top-down fashion, may suppress benthic invertebrate populations and activity, and thus indirectly augment algal growth. Exotic crayfish may reduce macrophytes and thus deplete associated meio- and macrofaunal populations (38). The zebra mussel monopolizes some freshwater sediments, altering water quality and depleting food for other filter feeders (39).

Pulse disturbances in lotic systems include floods, chemical spills, substratum and wood movement, rapid temperature changes, and bank slumping. In lentic systems, pulses include storms with consequent wave action, inputs of chemicals, deoxygenation, and rapid changes in turbidity. Inputs of chemicals, deoxygenation, and alteration of sediment characteristics are common disturbances to groundwaters, especially in urbanized or highly modified catchments. Most press disturbances in freshwater sediments are also catchment-mediated, e.g., sedimentation, nutrient leakages, increased light and temperature due to damage to riparian vegetation, and loss of organic matter inputs. Ramp disturbances are those that once started, steadily build in magnitude and may thus change in character with time—many human interventions on catchments give rise to ramps. Greenhouse disturbances may be ramps acting over long time periods to alter water flow and biological processes in freshwater sediments.

The biotic response to disturbance can be divided into *resistance,* or the capacity to withstand a disturbance, and ***resilience***, the capacity to recover from a disturbance (40). The response to a disturbance varies considerably among groups of benthic organisms with microbial groups probably exhibiting the greatest resistance and resilience (Table 5). Because disturbances dramatically alter species composition in freshwater sediments, biotic links are usually weakened and ecosystem processes may be severely impaired (33). In running waters, resilience is fairly high because recovery and recolonization are relatively predictable and rapid, so long as colonists are available within the catchment (41). In lakes and groundwaters, resilience of the sediment fauna is generally reduced because of their isolated nature and sensitivity to physical alteration, but resilience could be high in alluvial coarse sediment (42).

Although studies of species responses to disturbance are common, at least for the larger benthos, few studies have examined the response of system *processes* to disturbance. Of those studies completed, experimental acidification did not affect decomposition in lake sediments but did reduce macro-detritivores, whereas experimental eutrophication of lakes increased the production of cyanobacteria (blue-green algae) and increased both sulfate reduction and methanogenesis (33). In lakes, there appears to be very little redundancy in macro-detritivores and members of this group, such as crayfish, are very susceptible to disturbance (43). In flowing waters, both floods and the addition of pesticides have been shown to alter particulate organic matter dynamics (44), reduce shredder activity (45), and deplete primary and secondary production (46).

Thus, the benthic biota of freshwater sediments are greatly affected by disturbances (exhibit low resistance) with groundwater and lentic ecosystems taking the longest to recover (exhibit lowest resilience). Disturbances have also been shown to alter ecological processes in freshwater sediments although the link between the disturbance-induced loss of individual functional groups or species and altered ecosystem processes needs much more study. It is worth noting that many benthic macroinvertebrates are quite susceptible to disturbances and yet for some groups, e.g., bioturbators, shredders, their functional redundancy may be low. This once again implies that the loss of species of bioturbators and shredders from freshwater sediments may lead to serious ecosystem degradation.

AN INTERNATIONAL RESEARCH AGENDA

Despite its importance to freshwater science and human welfare, sediment biodiversity and the roles sediment biota play in freshwater ecosystems are known only in broad outline (Tables

Table 5. Impact of disturbance on freshwater sediment biota as indicated by probable relative resistance and resilience of important functional groups. Groups are listed in the order of high to low resistance, but note that resilience does not follow the same pattern. Since species in these groups play key roles in freshwater ecosystems and their loss may result in environmental degradation, future research should focus on those species within groups that are the most vulnerable to disturbance, i.e., those with the lowest resistance and resilience. Hypothesized resistance/resiliency of groups based on a variety of sources and authors' consensus from SCOPE workshop.

Functional group	Relative resistance	Relative resilience
microbial respirers	high	high
detritus collectors	some high (e.g., simuliid larvae) some low (e.g., hydropsychid caddis larvae)	moderate to high
algae	moderate	high
detritus processors (e.g., shredders)	low	low
biofilm producers	low	moderate
macrophytes	low	low
bioturbators and sediment stabilizers	lowest	lowest

2, 3, 4). If we are to effectively manage freshwater ecosystems, we must understand freshwater sediment biodiversity much better. We believe that action is urgently needed especially in three areas: *(i)* documenting sediment biodiversity; *(ii)* investigating the links between sediment biodiversity and freshwater ecosystem functioning; and *(iii)* protecting biodiversity.

Documenting Biodiversity in Freshwater Sediments

We know only generally how many species live in the world's freshwater sediments (Table 2), what traits they possess, and what processes they participate in (Table 4). Because of accelerating extinction rates, it is critical that we redouble our efforts to discover and describe the natural history of the many unknown species in the world's freshwaters sediments. Bacteria, fungi, and small invertebrates are particularly poorly known and deserve special attention; likewise, groundwaters and wetlands are habitats that will need careful investigation. Because most scientific work has focused on Europe and North America, much remains to be done in other parts of the world. As part of an initiative to describe the freshwater sediment biota, we desperately need to train many more competent taxonomists and natural historians, especially in Africa, Asia, and South America. Without an immediate, aggressive training effort, many more freshwater species will disappear before we discover or understand even the most basic facts about them.

Investigating Linkages Between Biodiversity in Freshwater Sediments and Ecosystem Processes

Clearly, species affect ecosystem functioning, but our understanding of the linkages between biodiversity and ecosystem processes are very incomplete. There is much scope for progress here, particularly in determining the sensitivity of ecosystem processes to loss of freshwater sediment species in different functional groups. Initially, we suggest focusing on sediment taxa which contain few species, but which play critical roles in freshwater ecosystem functioning. Examples that we have identified include bioturbators that mix the sediments, animals that shred or break apart organic matter, and anaerobic eurkaryotes that play key roles in nutrient cycling and water cleansing. While descriptive, comparative studies should provide useful information, we believe that experimental addition or removal of key species will provide the best tests of hypothesized linkages between sediment biodiversity and ecosystem functioning. Ideally, such experiments should be repeated in various habitats around the world, using a standard set of protocols. The experiments should be set up at sites where information on sediment biodiversity or ecosystem processes already exists. It may be useful to coordinate such efforts under the auspices of an international organization such as ILTER.

Protecting Freshwater Sediment Biodiversity

In many parts of the world, biodiversity in freshwater sediment ecosystems is under severe pressure from human activities. For example, in North America, many species of shellfish are in peril of extinction. We need to better publicize the importance of areas of high endemism or high diversity of freshwater sediment species (biodiversity "hotspots") and protect them from the most damaging human activities, e.g., dam-building, excessive water withdrawals. Further, we need to better recognize and control global threats to freshwater biodiversity such as human-induced climate change and the poorly controlled introduction of exotic species, both of which have serious, widespread consequences for the long-term integrity of the freshwater sediment biota. Until human impacts on freshwater ecosystems are better managed, we will continue to suffer unacceptably large losses of species and capricious alterations to ecosystem functioning.

Research Priorities for Freshwater Sediments
(More detail is provided in the text)

Document biodiversity, especially the most poorly known species, e.g. bacteria, fungi and small invertebrates.

Investigate linkages between biodiversity and ecosystem functioning.

Identify and publicize habitats in need of greatest protection, including areas of high endemism or high diversity and identify management strategies for conservation.

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60. Acknowledgements. The authors are grateful to the freshwater domain editorial committee: Alan Covich, Sam Lake, David Strayer and Janine Gibert.

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