Linkages between Aquatic Sediment Biota and Life Above Sediments as Potential Drivers of Biodiversity and Ecological Processes

MARGARET A. PALMER, ALAN P. COVICH, SAM LAKE, PETER BIRO, JACQUI J. BROOKS, JONATHAN COLE, CLIFF DAHM, JANINE GIBERT, WILLEM GOEDKOOP, KOEN MARTENS, JOS VERHOEVEN, AND WOUTER J. VAN DE BUND

A great deal of attention has been given to declining species diversity in terrestrial systems, and certainly the rate of species loss in tropical forests is staggering. Recently, increasing attention has been focused on the loss of species in aquatic ecosystems. Indeed, Ricciardi and Rasmussen (1999) report that freshwater extinctions in North America far exceed extinctions in terrestrial environments. For example, an increasing number of freshwater fish and bivalves are being added to endangered species lists (Angermeier and Schlosser 1995, Strayer et al. 1996). In contrast to our knowledge of fish and bivalves, information on species extinctions or even inventory lists are lacking for most inhabitants of the bottom sediments of lakes, streams, ground waters and wetlands, even though these "invisible" habitats harbor diverse and abundant biota (e.g., estimated at more than 100,000 species of sediment invertebrates globally, 10,000 species of algae, and more than 20,000 species of protozoans and bacteria; Palmer et al. 1997). Although the local and global environmental

> A DISRUPTION OR INTENSIFICATION OF THE DIRECT AND INDIRECT CHEMICAL, PHYSICAL, OR BIOLOGICAL INTERACTIONS BETWEEN AQUATIC SEDIMENT BIOTA AND BIOTA LIVING ABOVE THE SEDIMENTS MAY ACCELERATE BIODIVERSITY LOSS AND CONTRIBUTE TO THE DEGRADATION OF AQUATIC AND RIPARIAN HABITATS

Margaret A. Palmer (e-mail: mp3@umail.umd.edu) is a professor in the Department of Biology at the University of Maryland, College Park, MD 20742. Alan P. Covich is a professor in the Department of Fishery and Wildlife Biology at Colorado State University, Fort Collins, CO 80523. Sam Lake is a professor in the Department of Ecology at Monash University, Clayton, Victoria 3168, Australia. Peter Biro is a research scientist at the Balaton Limnological Research Institute, Tihay POB 35, Hungary. Jacqui J. Brooks is a postdoctoral associate in the Department of Biology at the University of Maryland, College Park, MD 20742. Jonathan Cole is a scientist at the Institute of Ecosystems Studies, Cary Arboretum, Millbrook, NY 12545. Cliff Dahm is a professor in the Department of Biology at the University of New Mexico, Albuquerque, NM 87131. Janine Gibert is a professor in the Department of Ecology at the University of Lyon, Villeurbanne cedex, France. Willem Goedkoop is a professor in the Department of Environmental Assessment at the Swedish University of Agricultural Sciences, Uppsala SE-75007, Sweden. Koen Martens is a scientist with the Royal Belgian Institute of Natural Sciences, Brussels B-1000, Belgium. Jos Verhoeven is a lecturer in the Department of Geobiology at Utrecht University, 3508 TB Utrecht, The Netherlands. Wouter J. van de Bund is a scientist at the Netherlands Institute for Ecology, Centre for Limnology, 3600 BG, Maarssen, The Netherlands.

consequences of species extinctions in aquatic sediments are not fully understood, many sediment species are likely to play important functional roles in freshwater ecosystems (Covich et al. 1999). Sediment biota not only mediate biogeochemical transformations of global significance but are essential to the maintenance of clean water, the decomposition of organic material (often added in excess to our water bodies), the uptake and transfer of materials (including sediment-bound contaminants), and primary production (Freckman et al. 1997).

Land-use changes and concomitant changes in the quality of water overlying aquatic sediments are contributing to the loss of sediment-dwelling species in freshwater ecosystems. Riparian plant communities are dwindling as urbanization and agriculture alter land use, and this decline in riparian zones has dramatic effects on nearby water bodies and their bottom sediments. Invertebrates that were previously abundant in lakes and streams are disappearing as the quality and quantity of groundwater and surface waters diminish (Richter et al. 1997). In North America alone, freshwater mussels are expected to experience future extinction rates of more than 6% per decade, and freshwater crayfish of nearly 4% per decade (Ricciardi and Rasmussen 1999). Taxa such as freshwater mussels and crayfish living on or near the surface of bottom substrates have been reasonably well studied. In contrast, there are so few data on the more cryptic freshwater sediment dwellers (e.g., worms, insect larvae) that estimates of extinction rates are not possible and mechanisms leading to extinction are poorly understood. The relationship between the loss of terrestrial and water-column species and the loss of aquatic sediment species is unknown. Are species losses in aquatic sediments linked to biotic processes and patterns aboveground? Is biodiversity in aquatic sediments threatened by the loss of species in adjacent terrestrial habitats or in the overlying water? Conversely, if sediment-dwelling species were lost, would the result be subsequent losses of flora and fauna in the water or in nearby terrestrial regions?

We explored such questions during a series of working groups organized by the Scientific Committee on Problems in the Environment (SCOPE). These questions are difficult to answer because research has not focused directly on links between biodiversity above ground and biodiversity in aquatic sediments, and because there are few quantitative studies on the diversity and functional roles of biota in aquatic sediments. In this article, we identify potential mechanisms that could lead to a coupling of above-sediment (terrestrial and water column) biota and the biota of aquatic sediments (sediment biota).

We hypothesize direct and indirect physical, chemical, and biological linkages between the flora and fauna living above sediment and the species composition in aquatic sediments. Because the magnitude of these linkages is largely unknown, parts of this article are speculative and meant to stimulate experimental studies or syntheses of existing data to explore this issue. If there is a tight coupling of above-sediment and sediment biodiversity in fresh waters, there may be a need to examine land management practices in the light of this knowledge. Further, if the diversity of aboveground species such as littoral plants is predictive of the diversity of aquatic sediment biota, then scientists may be able to use above-sediment diversity as a surrogate indicator of species diversity for aquatic sediments. This is attractive because sampling and identifying cryptic sediment biota is extremely difficult.

Aquatic sediments and above: Habitats and biota

The belowground habitats of freshwater systems include the sediments of both running waters (streams and rivers) and standing or semi-standing waters (wetlands, marshes, ponds, lakes, and ground waters) (Figure 1). The term "sediment" is broadly defined to include all unconsolidated material that makes up the bottom of aquatic ecosystems, including fine silts, sands, loose cobble, boulders, and partially or fully buried organic matter. All freshwater bodies are more or less connected to ground water through the hyporheic zone (the saturated sediments under and laterally adjacent to freshwater bodies where there is active exchange between ground water and surface water). The sediment–water interface is where the water-saturated sediment meets the water column. In aquatic ecosystems such as lakes, this interface may be obvious, whereas the distinction between the sediment and the water column is less clear and more variable over time in high-energy streams and rivers. While many aquatic organisms spend their entire lives in the sediment or in the water, many others live at the interface or spend part of their time in the water column and part in the saturated sediments. Further, some aquatic fauna (especially insects) spend part of their life cycle on land or in the air.

In this paper, we broadly define sediment biota as those organisms living within aquatic sediments, on aquatic sediments, or closely associated with aquatic sediments at some stage of their life. Thus, organisms that burrow in stream and lake beds, such as dipteran larvae, are sediment organisms, even though they may make diel migrations into the water column and spend their adult life flying and mating in the air or on trees. Similarly, organisms living on and among rocks in a stream are sediment biota because rocks are part of the unconsolidated stream bed. The definition of above ground biota seems relatively clear in terrestrial systems: grasses, trees, and animals that tower over the soils are clearly above ground. For freshwater ecosystems, the distinction between "above" and "below" is not as obvious because aquatic sediments may be covered by water (e.g., lakes) or by soil and plants, as in groundwater sediments and wetlands. Thus, organisms continuously inhabiting the water column (fish, plankton, macrophytes) above freshwater sediments are above-sediment biota. Likewise, terrestrial flora and fauna that border waterways or are in contact with the ground water that directly feeds the waterways are above-sediment biota. Macrophytes have roots that penetrate

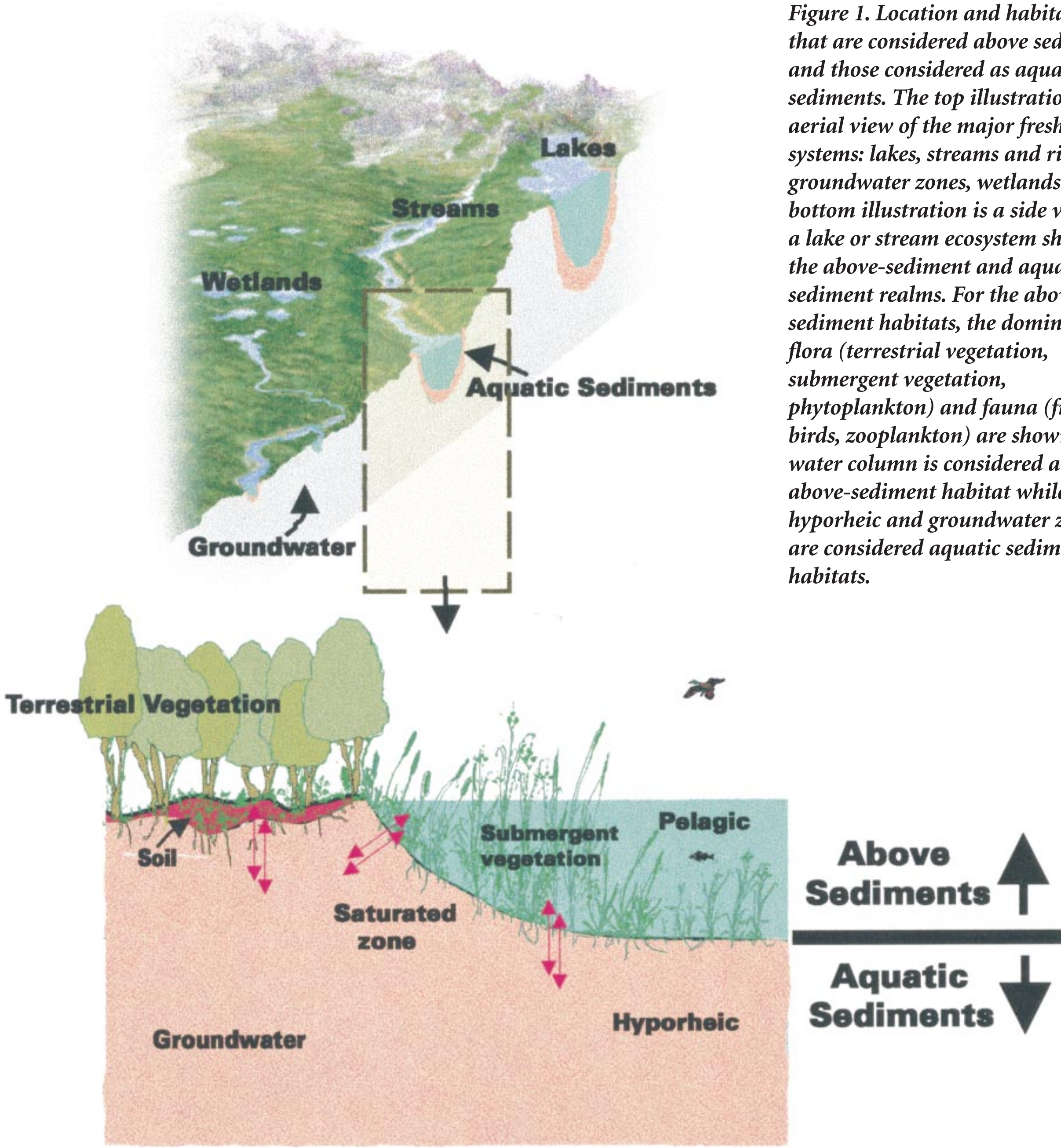

Figure 1. Location and habitat types that are considered above sediment and those considered as aquatic sediments. The top illustration is an aerial view of the major freshwater systems: lakes, streams and rivers, groundwater zones, wetlands. The bottom illustration is a side view of a lake or stream ecosystem showing the above-sediment and aquatic sediment realms. For the above-sediment habitats, the dominant flora (terrestrial vegetation, submergent vegetation, phytoplankton) and fauna (fish, birds, zooplankton) are shown. The water column is considered an above-sediment habitat while the hyporheic and groundwater zones are considered aquatic sediment habitats.

freshwater sediments and thus also could be considered sediment biota; however, by analogy with trees and other terrestrial plants that are considered part of the aboveground landscape (Hooper et al. 2000), ecologists treat macrophytes as above-sediment biota.

Biodiversity in aquatic sediments is poorly known, particularly for the smallest biota. For some freshwater systems, there is information on the number of sediment species for a few taxonomic groups (e.g., Bivalvia, Crustacea) or a few functional groups such as primary producers, but usually little more is known. The most numerous taxa in aquatic sediments (Table 1) are microscopic and often live deep within the sediments, making them difficult to sample. Even if samples can be obtained, few scientists have sufficient taxonomic expertise to identify collected specimens. Attention given to the Archaea, fungi, protozoans, and small, soft-bodied invertebrates of aquatic sediments has been especially inadequate (Palmer et al. 1997). Global estimates of microbial biodiversity in aquatic sediments remain highly controversial (Fenchel and Finlay 1995) and there are only a few published accounts of the genetic diversity of freshwater sediment bacteria and Archaea (Miskin et al. 1998, 1999). Instead, inferences about which bacterial functional groups are active are drawn from the type of biogeochemical process occurring (e.g., sulfate reduction, methanogenesis; Table 2), but these groups are rarely linked to diversity or even species units (Staley and Gosink 1999). In this article, we take a broad approach to aquatic sediment diversity, making use of the many diversity descriptors available (e.g., species richness, species composition, functional group diversity and composition).

The context and nature of linkages

Inputs from the air and watershed provide the milieu in which the interactions between above-sediment and aquatic sediment biodiversity are played out. Nutrients that fuel freshwater systems and influence primary productivity and species composition in aquatic sediments come largely from the watershed. Factors limiting the rate of decomposition in fresh water are also closely tied to the watershed and the air because input from these two realms may control the availability of electron acceptors such as sulfate and nitrate. These acceptors may determine the species composition and activity levels of aquatic sediment microbes that control decomposition rates. Geochemical links between land and water may also determine species composition in aquatic sediments. For example, the amount of bicarbonate weathered from rock and soil controls alkalinity in many aquatic systems, and bicarbonate alkalinity is a master variable in making water tolerable to a wide range of species. In sum, the large landscape context is important because interactions between the terrestrial or water column biota and sediment biota may depend to a major extent on the conditions set by watershed and aerial inputs.

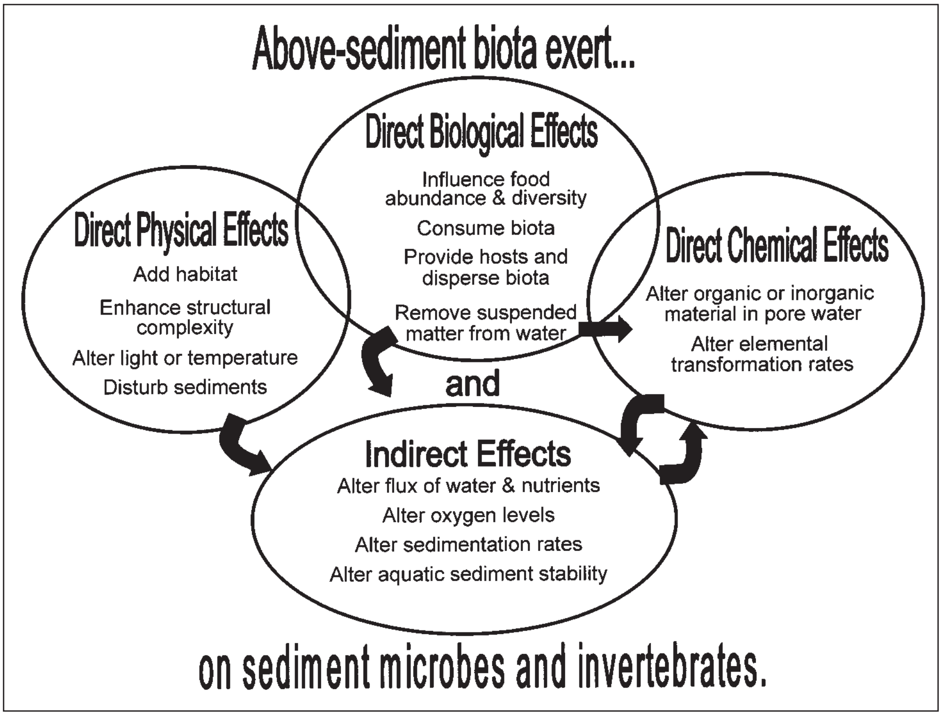

Figure 2. Major types of linkages between above-sediment biota and aquatic sediment biota (microbes and invertebrates). Arrows between spheres indicate that direct effects may lead to indirect effects (and in some cases, vice versa) that may also have dramatic effects on the sediment biota.

Table 1. Species richness of freshwater sediment biota. The number of species varies considerably between wetlands (up to 1500 species of invertebrates at a locale), lakes and streams (approximately 80–1000 species typically at a locale), and groundwaters (0–150 at a locale). Diversity also varies within a locale over time with, for example, low diversity in streams during flood season and high levels of diversity across the entire year. Estimated local species richness modified from Palmer et al. 1997. Aschelminthes includes gastrotrichs, nematodes, and rotifers.

Taxon	Typical local species richness
Algae	0–1000
Fungi	50–300
Protozoa	20–800
Plants	0–100
Invertebrates	30–1500
Aschelminthes	5–500
Annelida	5–50
Mollusca	0–50
Acari	0–100
Crustacea	5–300
Insecta	5–400

Because species-specific information is typically lacking for sediment biota, a functional group approach is useful for examining interactions among aquatic sediment organisms and those living above sediments (Table 3). For example, the diversity of above-sediment primary producers near wetlands may be linked to the diversity of detritivorous sediment biota because detritivores influence nutrient regeneration. Categorizing the many ways in which biota living in one realm may influence organisms in the other realm is difficult because there are numerous direct and indirect linkages between the biota and the physical processes (Figure 2). For example, the roots of macrophytes may provide new habitat for sediment biota and thus have a direct physical effect on sediment microbes and invertebrates. However, roots can also lead to an increase in porosity of aquatic sediments, which enhances oxygen penetration into sediment (an indirect chemical mechanism that affects sediment biota). This subsequently stimulates sediment microbial and invertebrate activity (a direct biotic effect), which may in turn alter porewater chemistry. Altered porosity, oxygen levels, microbial growth, and porewater chemistry can all influence biodiversity above and within the sediments. Despite these complexities, an organizational scheme that distinguishes direct from indirect effects and physical from biological and chemical effects is a useful heuristic tool for identifying and investigating links between aboveground biota and sediment biota (Figure 2). For example, one might design experiments to determine whether diverse fish assemblages are associated with diverse sediment fauna because a diverse sediment fauna offers a wider variety of prey for the fish, or because it increases spatial variability in sediment stability and facilitates a variety of spawning habitats that may be used by fish.

The influence of above-sediment plants on aquatic sediment biota

The role of terrestrial plants, especially those in the riparian zones of streams, and the role of macrophytes in aquatic ecosystem processes have been studied extensively (Carpenter and Lodge 1986, Gregory et al. 1991, Naiman and Decamps 1997). For this reason, we identified numerous mechanisms by which above-sediment plants may influence aquatic sediment biodiversity. Plants have direct structural effects on aquatic sediment habitats; they may affect sunlight penetration to the bottom, hydrology, food resources, and the chemical and microbial environment (Figure 2).

Structural effects. Submerged and emergent plants create habitat and add complexity to existing sediment habitat. The physical presence of plant structures in the water alters flow, enhances sedimentation rates, reduces the flux of nutrients across the sediment-water interface, and creates complex oxic–anoxic boundaries (Humphrey and Stevenson 1992). Reduced flow, enhanced sedimentation, and lowered oxygen may reduce the diversity of sediment invertebrates, particularly burrowers (Gregg and Rose 1982). However, it is likely that microbial biodiversity is rarely, if ever, reduced. Indeed, an abundance of oxic–anoxic boundaries may be associated with enhanced microbial diversity because different taxa, such as nitrifiers and denitrifiers or sulfate reducers and sulfide oxidizers, live in close proximity (Fenchel and Finlay 1995).

Above-sediment vegetation also directly influences sediment biota because plant stems and roots increase habitat complexity and sediment stability in aquatic systems. The presence of aquatic plants is generally associated with an increase in the abundance or species richness of many sediment-dwelling invertebrates (Soszka 1975, Gregg and Rose 1985, Rundle and Ormerod 1991). In temporary pools, root structure may contribute to the persistence of sediment fauna via promotion of seed and egg banks (e.g., the retention of encysted protozoans and invertebrates is enhanced in the presence of roots; Williams 1987). In running waters, roots also act to stabilize sediments (Keast 1984), which can then support a more diverse biota than sediments that are continuously moved by flow. Thus, the general effect of plants in freshwater ecosystems is to enhance diversity of sediment fauna (Sand-Jensen 1998).

Wood derived from terrestrial plants also enhances environmental heterogeneity in lakes and streams by creating diverse bottom habitat; the presence of wood in freshwater systems is usually associated with an increase in biodiversity of stream bottom invertebrates (Benke et al. 1985, Hax and Golladay 1993). The wood itself may decay, leaving "hotspots" of organically rich sediments, or the wood may alter the flow and sedimentation patterns to create patches of fine sediments interspersed with patches of coarser material. In streams, the net result may be an increase

Table 2. Major functional groups of freshwater sediment bacteria. Photosynthetic bacteria and nitrogen fixers are not shown because they do no fit into this metabolic organization scheme. Functional groups 1–5 are heterotrophic, and groups 6–9 are chemoautotrophic.

Common name of functional group	Electron donor	Electron acceptor	Environment where important
1. Aerobic heterotrophs	Organic (C) compounds	Oxygen	All oxic
2. Denitrifiers	Organic (C) compounds	Nitrate	Hypoxic/anoxic receiving NO_3 input
3. Manganese-Iron reducers	Organic (C) compounds	Fe^{3+}, Mn^{4+}	Anoxic
4. Sulfate reducers	Organic (C) compounds	SO_4	Anoxic, with sulfate
5. Fermenters	Reduced organic compounds	More oxidized organic compounds	Most environments, prevalent in anoxic
6. Methanogens	Acetate, H_2	CO_2	Anoxic
7. Nitrifiers	Ammonia	Oxygen (several steps)	Aerobic, non-anoxic interface, NH_4 present
8. Sulfur Oxidizers	Sulfide, elemental S, thiosulfate	Oxygen (and others, esp. Fe^{3+}, anaerobically)	Aerobic, near-anaerobic interface
9. Iron Oxidizers	Fe^{2+}	Oxygen	Aerobic, near-anaerobic interface

in species diversity of small sediment-dwelling invertebrates compared to stream sites with homogeneous sediments (Palmer et al. 1995). Because much of the wood in freshwater systems is buried, it creates unique habitats for many hyporheic microbes and invertebrates (Anderson and Sedell 1979, Smock et al. 1992). Wood and associated fungi and bacteria may also be eaten by specialized insects that would not typically be found in aquatic sediments (Batzer et al. 1999).

Shading effects. Large wetland and riparian plants influence the intensity and quality of light penetrating nearby fresh waters (Carpenter and Lodge 1986). The degree of shading of streams and nearshore standing waters is a function of the source and composition of terrestrial vegetation (Gregory et al. 1991). If levels of shading are too high, whole functional groups of sediment biota such as algal-feeding invertebrates may disappear, causing a decline in sediment diversity. Loss of even a few species of plants may have direct effects on sediment biodiversity through the loss of shade-tolerant algal species or the loss of temperature-sensitive sediment biota (Gregg and Rose 1982). Aquatic plants, particularly planktonic algae, also exert strong shading effects that can reduce sediment algal diversity, which, in turn, may have cascading effects throughout running water and lake food webs (Sand-Jensen and Borum 1991, Scheffer 1998).

Hydrologic effects. Freshwater sediments are linked to terrestrial soils and to surface waters through hydrological interactions between the ground water and the surface water. These hydrologic processes are tightly coupled to the population densities and species composition of aboveground vegetation, which in turn have feedback effects on the flux of water and materials in soils. Terrestrial vegetation may thus control or constrain ecological processes in lakes, streams, and rivers by influencing the quality and quantity of water inputs that have passed through the adjacent soils (Gregory et al. 1991, Dahm et al. 1998). In running water systems, submerged macrophytes can cause local downwelling and upwelling zones in the sediments that may have significant effects on the hyporheic microbes and invertebrates. The biota of aquatic sediments are known to be extremely sensitive to hydrologic alterations; changes in species and functional group composition and richness are expected with changes in water levels, flow magnitude, flood frequency, and groundwater quality (Hildrew and Townsend 1994, Dahm and Valett 1996, Gibert et al. 1997, Lake 1998, McCabe and Gotelli 2000).

Food resource effects. The food webs of many aquatic ecosystems are supported largely by input of plant material

Table 3. A functional group approach to categorizing the influence of above-sediment biota and nonmicrobial aquatic sediment biota on ecological processes in the adjacent realm. Since many aquatic sediment species belong to multiple functional groups or change in response to environmental factors or life stage, the species composition within a functional group is not considered fixed.

Functional group	Effect on adjacent realm	General examples
	Above-sediment biota exerting effects on aquatic sediments	
Primary producers	Provide food and habitat for sediment fauna Alter sediment properties	Macrophytes, terrestrial vegetation, epiphytic algae, phytoplankton
Herbivores	Consume sediment diatoms and attached algae	Plant epiphytic fauna, zooplankton, fish
Predators	Consume sediment-dwelling animals Disturb sediment	Birds, fish, otter
Detrital processors	Mechanically and chemically break down dead organic matter, some of which is transported to the sediments	Epiphytic fauna, zooplankton, fish, fungi
Bioturbators	Physically and chemically alter sediments Resuspend sediment fauna Create new habitat	Hippos, beavers, fish
	Aquatic sediment biota exerting effects above sediment	
Primary producers	Provide food for pelagic and terrestrial herbivores	Diatoms, filamentous algae
Herbivores	Consume macrophytes Alter/destroy plant structures	Grazing invertebrates, protozoans
Predators	Consume above-sediment animals	Invertebrate suspension feeders
Detrital processers	Mechanically and chemically break down dead organic matter	Shredding and scraping insects, invertebrate suspension feeders
Biofilm producers	Alter flux of nutrients from the sediment to the water and to adjacent terrestrial soils Bind soils/sediments	Diatoms, microbes, snails

Figure 3. Inputs of terrestial leaf material support the food webs of many freshwater ecosystems such as this low-gradient stream. Leaves may cover streambeds just after autumn leaf fall but are broken down and incorporated into aquatic sediments by microbes and invertebrates. Photo: David Hinkle.

from the surrounding landscape (Figure 3). Plant litter influences the abundance and diversity of sediment-dwelling microbes and invertebrates in freshwater sediments (Gregory et al. 1991, Glova and Sagar 1994, Wallace et al. 1997). For example, stream bottom invertebrates are influenced by the composition of riparian leaf litter, and some have species-specific relationships with macrophytes or algae (Webster and Benfield 1986, Cummins et al. 1989, Cronin et al. 1999). Although rigorous experimental tests are still in progress, it is widely believed that high plant diversity above ground (e.g., in riparian zones) and in the water may promote greater diversity in aquatic sediments via resource effects (Figure 4). This belief extends from the understanding that a diverse assemblage of plants should increase the period during which high-quality detritus is available to aquatic bottom-dwelling consumers, increase the diversity of epiphytic algal food sources, and enhance the diversity of dissolved organic substrates, which in turn promotes enhanced microbial diversity (Polunin 1984, Rosemond 1994, Kaplan 1998). Attempting to link the diversity of organic carbon sources to the diversity of sediment biota is difficult because of the many potential mechanisms underlying putative linkages and because many factors other than these linkages influence biodiversity in aquatic sediments. To date, studies do suggest that some stream invertebrates have preferences for, and higher growth rates on, certain species of decomposing leaves (Leff and McArthur 1989, Stanko-Mishic et al. 1999, Palmer et al. 2000), supporting the hypothesis that a high diversity of aboveground plants may indeed promote greater biodiversity in aquatic sediments. This is certainly an area in which creative experiments are needed.

Diversity of live vegetation may also be an important determinant of aquatic sediment biodiversity. In wetlands and lakes, many species of sediment invertebrates use submergent and emergent vegetation as food or as structures on which to graze or live. The stems of aquatic plants host rich diatom and microbial communities that serve as an important food source for invertebrates, even many sediment dwellers (Carpenter and Lodge 1986). Sediment biota that make forays out of the sediments may take advantage of the plants themselves as food or may graze on the diatoms and microbes growing on the plant stems (Lodge 1991, Newman 1991). To date, studies examining macrophyte and invertebrate diversity have focused mainly on invertebrates living on plants (epiphytic invertebrates), not on invertebrates living in the sediments surrounding plants. Thus, whether or not a high diversity of aquatic plants promotes a high diversity of sediment biota remains to be tested.

Chemically and microbially mediated effects. Plants influence not only the flux of water to aquatic sediments but also influence the composition of water moving into nearby water bodies. Changes in plant species can dramatically alter water chemistry, particularly the amount and form of nitrogen, phosphorus, and carbon, which may in turn influence the sediment-dwelling biota (Carpenter and Lodge 1986, Haycock and Pinay 1993, Naiman and Decamps 1997).

Vegetative alteration of nitrogen and phosphorus near bodies of water may be significant, depending on plant species, soils, and degree of saturation (Cole 1981, Peterjohn and Correll 1984). For example, Gregory et al. (1991) found that rates of denitrification in ground water were higher in alder-dominated stands than in conifer-, or

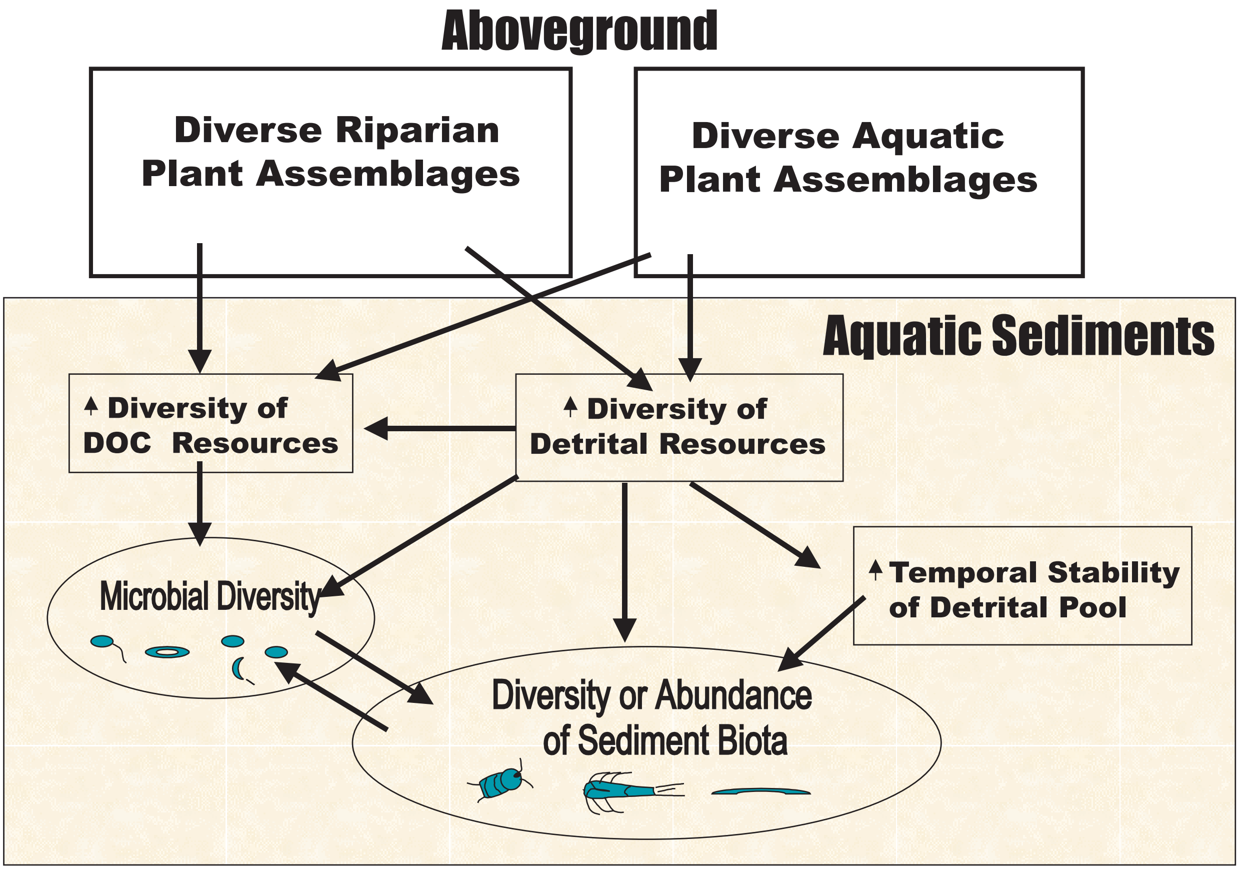

Figure 4. Hypothetical mechanisms by which diverse terrestrial (riparian) and aquatic plant communities may lead to an increase in the biodiversity in aquatic sediments. DOC: dissolved organic carbon; stability of detrital pool: temporal constancy in detrital food availability for consumers; diversity of detrital resources: number of different types of organic matter contributing to the detrital pool (e.g., leaf species that are chemically and structurally different); microbial diversity: number of functional or genetic groups of bacteria, fungi, and protozoans. Goose Creek (photo) in northern Virginia is typical of a healthy mid-Atlantic stream with high diversity of aquatic invertebrates and fish. Photo: David Hinkle.

herb/shrub-dominated stands. Similarly, certain species of macrophytes are known to remove inorganic carbon from the water both by assimilation into organic matter and by precipitation as carbonate salts on the leaves. These deposits can lead to the formation of mixed carbonate and silt sediments (marl sediments; Wetzel 1960), which may have distinct benthic communities.

To date, experiments have not explored the relationship between plant species richness and subsurface water chemistry, but clearly plant species composition has significant effects on the chemistry of aquatic sediments. Because bacteria respond dramatically to changes in their chemical environment, we predict rapid responses by the aquatic sediment microbial community to any change in plant species that affects sediment porewater chemistry. Input of nitrogen and carbon from vegetated regions into freshwater sediments stimulate aerobic, anaerobic, and chemolithotrophic sediment microbes (Duff and Triska 2000). Similarly, changes in nutrient levels have been shown to have marked effects on the species composition of aquatic sediment-dwelling algae (Pringle 1990, Rosemond et al. 1993). Since gradients in microbial function may correspond to chemical gradients (Findlay and Sobczak 2000), microbial biodiversity may also respond to changes in sediment chemistry that are linked to above-sediment plants (Figure 2).

The link to microbial biodiversity is speculative at this point, because the study of microbial species composition in aquatic sediments and its relation to microbial function is in its infancy (Findlay and Sobczak 2000). Bacteria are abundant both in water (more than 10^6/ml) and in aquatic sediments (more than 10^9/gdw) (Cole et al. 1988), although not all bacteria are metabolically active at any one time (Stevenson 1978, del Giorgio and Scarborough 1995). Despite differences in activity levels, essentially every metabolic functional group of microbes (Table 2) is found at some time and place in nearly every freshwater environment. Recent research employing coinjection of a conservative tracer (bromide) and a labile electron donor (acetate) in stream sediments has shown that the full suite of catabolic microbial processes occurs over scales of meters or less (Baker et al. 1999). Specifically, aerobic metabolism, denitrification, metal reduction, sulfate reduction, and methanogenesis all appear to vary over these spatial scales.

These results suggest that a diverse assemblage of bacterial functional groups coexists in freshwater sediments. Which of these groups are active may depend on plant biodiversity above the sediments, because plants influence sediment chemistry. Work by Dahm et al. (1998) has shown that the availability of specific forms of electron donors and electron acceptors in ground water affects microbial composition and dynamics in freshwater sediments. Under the appropriate conditions, one or more microbial functional groups may become active and dominant (Baker et al. 1999). Thus, functional diversity, and perhaps species diversity, of freshwater sediment microbes must be very dynamic over time and space, and may respond rapidly to changes in water chemistry induced by changes in the overlying plant species composition.

Whether or not chemical effects on the microbial community have cascading effects on the larger sediment-dwelling biota is an open question. The area is ripe for additional research; studies manipulating microbial diversity or composition—by manipulating porewater chemistry (Kaplan and Newbold 1995) and tracking the response by microbial consumers, for example—would provide insights into how tightly sediment biodiversity is coupled to aboveground plant diversity. Changes in the species or functional diversity of sediment microbes could influence the species composition of sediment-dwelling invertebrates, particularly meiofauna (invertebrates less than 500 μm), that graze selectively on microbes, such as algae and protozoans (Bott and Borchardt 1999, Hakenkamp and Palmer 2000). Because freshwater meiofauna may be consumed by macroinvertebrates, there is the potential for plant-mediated water chemistry effects to cascade from the bacteria to the protozoa and algae to the meio- and macrofauna.

The influence of above-sediment animals on aquatic sediment biota

Compared to the effects of plants, we identified fewer examples of terrestrial and pelagic animals influencing aquatic sediment biota. Certainly, terrestrial animals that forage in or move through fresh waters, such as hippopotamuses or beavers, may have dramatic effects on entire aquatic ecosystems, including the sediment biota. However, other above-sediment biota (e.g., fish) may routinely alter the biodiversity of aquatic sediment biota through their direct and indirect physical and biological effects.

Physical effects. Large terrestrial or pelagic animals influence sediment biota through their mechanical effects on aquatic sediments: beavers and fish can enhance habitat heterogeneity for sediment biota through their grazing and spawning activities (McDowell and Naiman 1986, Smith et al. 1991). Habitat heterogeneity is generally believed to increase the diversity of aquatic sediment biota; however, some large animals that frequent wetlands or streams (e.g., hoofed mammals) disturb the sediments so much that positive effects on sediment biodiversity are unlikely. Cattle moving in fresh waters trample vegetation, enhance siltation, and generally cause an overall reduction in sediment biodiversity, particularly because sensitive species of insects and crustaceans are lost (Waters 1995). In such settings, only a few species of highly tolerant fauna (e.g., midge larvae, tubificid oligochaetes) may dominate the aquatic sediments. While the mechanical effects of above-sediment fauna (such as beavers) have been documented for a few specific cases, general links between the diversity above sediment and in the sediment have not been explored.

Through their dam-building activities, beavers may enhance the deposition of fine particles to bottom sediments, creating anoxic conditions suitable for methanogenic bacteria. Ford and Naiman (1988) found that methane loss to the atmosphere was 33 times greater in ponds with beavers than in those without them, presumably because there was a shift in the below-sediment microbial community in favor of methanogens (see fermenters, Table 2). Beavers can also influence microbial diversity in aquatic sediments by increasing the proportion of nitrogen fixers in the microbial community. Because dams accumulate large amounts of litter, they also influence acidity and iron concentrations. Such chemical effects may have contributed to complex changes (often declines) in invertebrate diversity (Smith et al. 1991). In areas with dams, Smith et al. (1991) found, there were reductions in the diversity of some insect groups (especially caddisflies and stoneflies), although other sediment biota (especially dipterans) were more abundant or diverse.

Indirect effects. Shifts in the species diversity of sediment biota may be linked to the fecal input of above-sediment biota. This input can be substantial in ponds and wetlands and may enhance nutrient availability to the bottom fauna. For example, Pettigrew et al. (1997) showed that waterfowl fecal inputs had effects on primary production of freshwater bottom-dwelling algae, which in turn had differential effects on species of both pelagic and sediment-dwelling crustaceans. Feces from terrestrial and flying biota can also extend the geographical range of aquatic sediment-dwelling species that produce resting eggs. The eggs may be eaten by above-sediment biota, survive in their guts, and be deposited in new freshwater systems as the biota disperse (Williams 1987).

Predatory effects. Pelagic predators are probably the single most important above-sediment group that exerts direct biotic effects on aquatic sediment biota. Bottom-feeding fish and predatory invertebrates rely on many sediment species for their food, and the dramatic influence of these predators on the diversity of sediment biota is extremely well documented in freshwater systems (Allan 1995). Pelagic fauna also have nonconsumptive effects on below-sediment fauna, as they often disturb the sediment (by producing feeding pits, scars, spawning beds) and can dramatically influence invertebrate abundance and species composition in or on aquatic sediments (Field-Dodgson 1987, Flecker 1996). Further, the presence of pelagic predators may alter the behavior of prey in aquatic sediments and induce dispersal from the sediments to the water or surrounding littoral or riparian zone (Wooster and Sih 1995, McIntosh and Peckarsky 1996). Because many predators have strong selective preferences for certain sediment species, they can have dramatic influences on the temporal and spatial dynamics of species composition. The presence of macrophytes can mediate the impact of pelagic predators on sediment biota in fresh waters because the plant stems may impede predator movement and foraging near the bed (Bell et al. 1991). The negative effects of some above-sediment organisms (e.g., pelagic predators) can thus be offset by the positive effects of other above-sediment life (e.g., macrophytes). Pelagic biota may also influence biodiversity of sediment-dwellers via complex linkages among life cycles. For example, fish may limit bivalve diversity because many freshwater bivalves produce larval stages that require particular fish species as hosts (Hagg and Warren 1998).

The influence of pelagic algae on aquatic sediment biota

Planktonic algae are another important above-sediment form of life that may have a dramatic influence on sediment biodiversity, especially following algal blooms. For example, the type, and possibly the diversity, of phytoplankton that settles to the bottom influences the heterogeneity of carbon sources that serve as food for invertebrates and substrates for microbes (Goedkoop and Johnson 1996). The phytoplankton in moderately eutrophic lakes is characterized by a strong dominance of diatoms, especially during spring and autumn. Diatoms show high sinking rates, are rich in polyunsaturated fatty acids, and are considered a high-quality food for sediment-dwelling invertebrates (Johnson et al. 1989, Ahlgren et al. 1997). The nutritional value of different phytoplankton species affects the efficiency of energy transfer across trophic levels and may affect sediment biota in different ways. Additionally, planktonic cyanobacteria may release toxins or alter the water pH (Christoffersen 1996), both of which can have direct effects on sediment life after settling or when washed up in a littoral zone.

The influence of aquatic sediment biota on above-sediment biota

The mechanisms by which sediment-dwellers influence life above the sediments are less numerous and more difficult to identify than those by which the above-sediment biota influence sediment life. The most important effects of sediment biota on the terrestrial realm are probably related to water chemistry. Aquatic organisms that bioturbate sediments alter the flux of nutrients and oxygen into the water, changing the composition of pelagic bacteria and algae (Petr 1977, Polunin 1984, Johnson et al. 1989, Svensson and Leonardson 1996). Changes in water chemistry are also likely to influence vegetation and fauna living along the edges of water bodies; however, this has not been explicitly investigated. Certainly macrophytes living in aquatic sediments will be influenced by biotic activities that alter sediment chemistry or porosity (Barko et al. 1991).

Benthic biota living deep within marine sediments are well known to influence the concentrations of suspended matter that may dramatically alter growth of macrophytes, algae, and pelagic herbivores. Ecosystem-level effects of burrowing biota have been studied less in freshwater systems than in marine systems (Hakenkamp and Palmer 1999). However, there are dramatic examples of huge impacts by freshwater biota living at the sediment-water interface. Following the invasion of nonnative zebra mussels to water bodies in the United States, an 85% decrease in phytoplankton biomass and dramatic changes in algal and invertebrate species composition were documented for the Hudson River (Caraco et al. 1997, Strayer et al. 1999, Lake et al. 2000).

Sediment biota also contribute to the decomposition of organic matter; this in turn influences remineralization rates and nutrient availability to phytoplankton and macrophytes. Macroinvertebrate feeding and burrowing strongly enhance the processing of organic material (Gullberg et al. 1997). Sediment-living macroinvertebrates mechanically fragment particulate organic matter and bioturbate the bottom, both of which processes enhance rapid decomposition and nutrient turnover of sediment detritus. Macroinvertebrate burrowing results in a deeper oxygenation of sediments, thereby extending the aerobic habitat of the sediment. The result is higher bacterial activity (van de Bund et al. 1994) and a more complete remineralization of organic matter and flux of nutrients to the overlying water (Goedkoop et al. 1997, Herbst 1980). These effects may be particularly important in the context of the regeneration of specific nutrients, such as phosphorus and silica, which limit pelagic primary production.

Conclusions and future priorities

Given the functional importance of biota living in aquatic sediments and the difficulty of cataloging their diversity and distribution (Palmer et al. 1997), it is unfortunate that we know so little about regulatory linkages between sediment biodiversity and diversity above sediments. Basic research on the distribution and functional roles of benthic species is needed to develop models predicting the effect of environmental changes above ground on aquatic sediment biota. Because plants play critical structural, chemical, and biological roles in determining the species composition and distribution of sediment-dwelling organisms in lakes, wetlands, and running waters, particular attention should be focused on the plant–aquatic sediment linkage. The presence and diversity of terrestrial and aquatic vegetation may enhance biodiversity in freshwater sediments (Figure 4), but this supposition awaits rigorous testing.

The influence of terrestrial and pelagic animals such as ungulates, beavers, and fish on aquatic sediment communities can be both positive and negative; diversity or abundance of sediment biota may decline or be enhanced. The greatest gap in knowledge with respect to linkages between aboveground plants or animals and aquatic sediment biota relates to the microbial community. Little is known about the diversity of bacteria and protozoans in aquatic sediments, and much less about whether microbial distributions are affected by the diversity of plants or animals living above the sediments. Thus, a top research priority should be to document patterns in microbial biodiversity in aquatic sediments, particularly in geographic areas where terrestrial plants and animals are well described. Other important research priorities should be to enhance our understanding of the functional roles of sediment-dwelling species, including the smallest invertebrates, and to complete experiments to determine whether high above-sediment biodiversity acts to buffer nearby aquatic sediment communities from change.

Research in these areas is important because there are environmental management implications if linkages between above-sediment life and aquatic sediment biodiversity are found (Table 4). Any human activity that disrupts or intensifies the transfer of material (e.g., organic matter, nutrients, sediments, contaminants) from terrestrial areas to fresh waters or any activity that simplifies the landscape adjacent to water bodies may need regulation. Land use change is expected to have a dramatic global impact on biodiversity over the next 100 years (Sala et al. 2000). As Sala and colleagues emphasize, this effect will be most pronounced in freshwater ecosystems because humans live disproportionately near waterways and rely on them heavily for waste disposal, transportation, and water supply. Management decisions may be required to minimize groundwater withdrawals if such withdrawals decouple the movement of nutrients from soils to fresh waters (often via the hyporheic zone).

Land-use and management practices may need to be revised to focus on the maintenance of plant diversity adjacent to freshwater bodies, not only on the maintenance of a sizable plant buffer zone. Plant monocultures near fresh waters may result in dramatic declines in aquatic sediment biodiversity, because diverse plant communities provide diverse food, habitat, and shade for sediment biota. Declines in aquatic sediment biodiversity are also expected if road density near water bodies is not kept in check, because impervious surfaces interfere with groundwater movement and because road crossings may be associated with an increase in the introduction of invasive plant and animal species. Intentional and unintentional introduction of organisms into freshwater lakes is probably the single biggest threat to aquatic biodiversity, yet developing management strategies for addressing problems associated with exotic species is very difficult (Figure 2 in Sala et al. 2000). With the introduction of exotic species into fresh waters, the loss of native sediment species that play a disproportionate role in ecological processes in fresh waters ("keystone" species or groups) is of particular concern (Palmer et al. 1997, Covich et al. 1999). While the local and global consequences of the loss of keystone biota and of altered linkages between above-sediment and sediment biota are not fully understood, scientists agree that the decline of biodiversity in many fresh waters is staggering. Research efforts to elucidate the linkages and document their consequences are essential.

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Table 4. Priorities to ensure the maintenance of ecologically important linkages between freshwater sediment biota and life above the sediments. Each of the listed priorities has management implications; however, basic research on sediment biota and how they respond to a change in above-sediment biodiversity is needed.

Priorities	Examples of importance for sediment life
Avoid disruption of material transports between terrestrial and aquatic system	Undisturbed soils adjacent to fresh waters harbor distinct microbial species that can remove excess nutrients and pollutants. Excessive withdrawal of ground water can convert normally saturated riparian zone to one with dry, oxygenated soils; anaerobic microbial metabolism may be inhibited in such situations.
Maintain structural habitat complexity	Plant roots and wood provide habitat and food for sediment biota. These structures enhance environmental heterogeneity, sediment porosity, and oxygenation, all of which contribute to sediment biodiversity.
Preserve or restore diverse plant communities adjacent to freshwater bodies	Species-rich riparian zones and wetlands create habitat, shade, and diverse food resources (live plant tissue or detritus) for aquatic sediment biota.
Minimize establishment of invasive species	Minimizing accidental or intentional introduction of exotic fish prevents the competitive exclusion of native fish, which often results in cascading effects to the sediment biota.
Maintain conditions that are favorable for keystone groups of biota	Bioturbators oxygenate and increase soil permeability, which influences the flux of water, nutrients, and gases to aquatic sediments. Earthworms aerate soils and sediments, enhancing structural and biogeochemical complexity of aquatic sediments.

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