Physical and biological controls on fine sediment transport and storage in rivers

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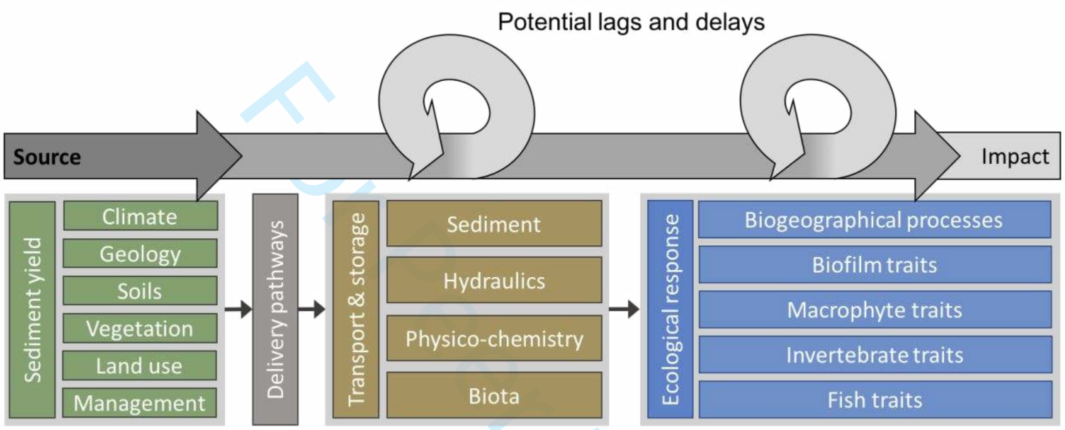
Abstract

Excess fine sediment, comprising particles <2 mm in diameter, is a major cause of ecological degradation in rivers. The erosion of fine sediment from terrestrial or aquatic sources, its delivery to the river, and its storage and transport in the fluvial environment are controlled by a complex interplay of physical, biological and anthropogenic factors. Whilst the physical controls exerted on fine sediment dynamics are relatively well-documented, the role of biological processes and their interactions with hydraulic and physico-chemical phenomena has been largely overlooked. The activities of biota, from primary producers to predators, exert strong controls on fine sediment deposition, infiltration and resuspension. For example, extracellular polymeric substances (EPS) associated with biofilms increase deposition and decrease resuspension. In lower energy rivers, aquatic macrophyte growth and senescence ~~is~~ are intimately linked to sediment retention and loss, whereas riparian trees are dominant ecosystem engineers in high energy systems. Fish and invertebrates also have profound effects on fine sediment dynamics through activities that drive both particle deposition and erosion depending on species composition and abiotic conditions. The functional traits of species present will determine not only these biotic *effects* but also the *responses* of river ecosystems to excess fine sediment. We discuss which traits are involved and put them into context with spatial processes that occur throughout the river network. Whilst strides towards better understanding of the impacts of excess fine sediment have been made, further progress to identify the most effective management approaches is urgently required through close communication between authorities and scientists.

Graphical/Visual Abstract and Caption



Controls on the delivery, transport and storage of fine sediment and the resulting ecological responses in river networks. From the sediment sources in the landscape to the ecological impact in the river, the transport of particles and the responses of biota are subject to potential lags and delays as sediment is temporarily stored and time is taken for local populations to reach critical life-stages where fine sediment limits survival.

Introduction

Excess fine sediment ('fines'), typically defined as organic and inorganic particles <2 mm in diameter, is one of the principal reasons for the failure of waterbodies to achieve good ecological status (GES) under the EU Water Framework Directive (WFD)[1,2]. In light of this, the recent finding that most lowland rivers in the UK are transport-limited, leading to saturation of ~~river beds~~streambeds with fine sediment[3], is of critical importance. We may safely assume that this result can be generalised to other similar environments worldwide. It implies that in-channel transport and storage processes are primary controls on the volume of fines stored on or within the ~~river bed~~streambed, whereas both exogenous (i.e. sediment supply) and endogenous processes (e.g. bioturbation) primarily influence the concentration of fine sediments carried in suspension and their flux through the river network. Greater understanding of these processes is urgently required. To facilitate progress in the primary research areas involved, we provide a synthesis of current knowledge on the physical and biological factors controlling the transport, storage and ecological impacts of fine sediment in river channels to complement recent reviews on catchment-scale, terrestrial processes (e.g.[4]).

In reviewing the factors that control fine sediment transport and storage in river channels, we emphasise biological controls as these have received far less attention than physical controls (e.g.[5]). Bottom-up, biologically-driven forces are increasingly recognised as important elements for understanding fluvial geomorphic processes[6]. We build upon this knowledge in the specific context of fines. Ecological impacts at organism- and community- levels, driven by top-down abiotic forces, have been reviewed in detail elsewhere[7–10] but how the ecological response to fine sediment is mediated by the structure and function of ecosystems across multiple levels of organisation is less well-understood. We therefore also include information on ecological resistance (ability to withstand perturbation) and resilience (ability to recover from disturbance) to fine sediment stress at the level of individual organisms to regional biogeographies. We mostly limit the discussion to processes occurring after the sediment has been delivered to the river channel but also present some exogenous processes insofar as they influence in-channel controls. Our discussion is structured according to the conceptual model in Figure 1, going beyond a recent review on infiltration ('colmation')[11] to provide a more holistic perspective on the fine sediment 'problem'.

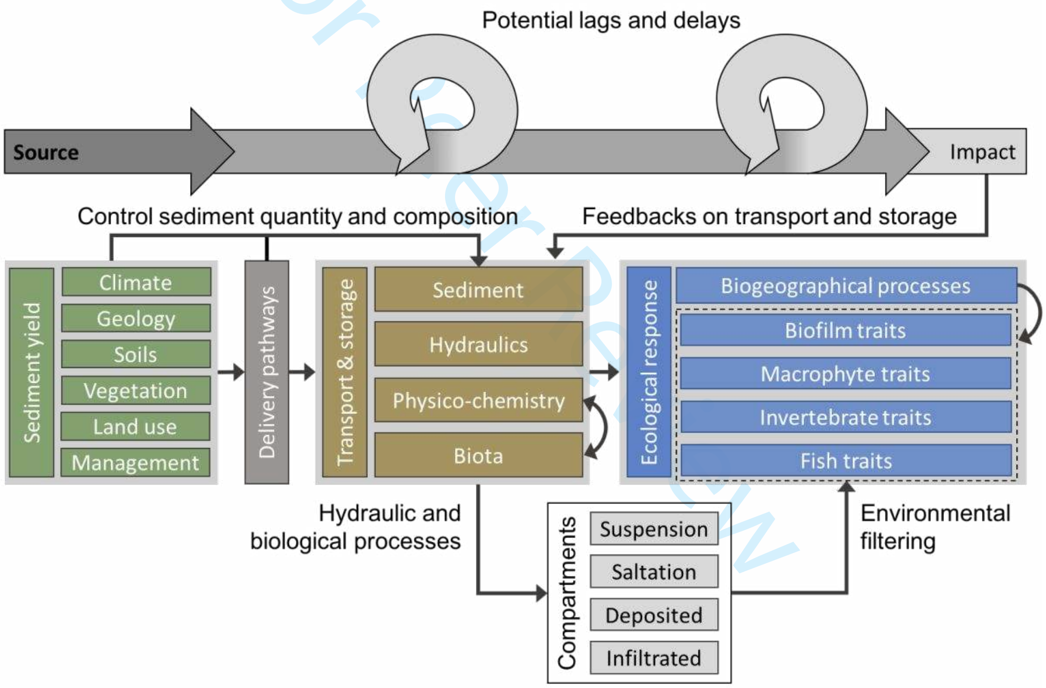


Figure 1 – Controls on the delivery, transport and storage of fine sediment and the resulting ecological responses in river networks. Natural and anthropogenic factors control the quantity and quality of sediment potentially available for delivery to the river channel. Whether or not this potential is realised, and the quantity and composition of sediment conserved during the pluvial phase, depends on delivery pathways that connect the source to the river channel. Once delivered to the river channel, particles may be transported through suspension or saltation, temporarily stored as surface-deposited material, or become infiltrated in the ~~river bed~~streambed and stored on a longer-term basis. Which compartment particles are transported or stored in depends on a number of controls, including the inherent properties of the particles, hydraulics, and the activities of biota. The latter is in turn influenced by

physico-chemical factors (e.g. oxygen, nutrients) that work to limit or enhance biological processes. The hydraulic and biological controls determine the compartments within which particles are transported or stored, structuring the physical habitat, modifying available resources and potentially filtering out unsuitable species from the species pool on the basis of their traits. Such environmental filtering effects may be interfered with by biogeographical processes related to dispersal. The fate of fine sediment, and the extent and nature of the impact it causes is subject to potential lags as sediment is temporarily stored within the landscape. Ecological impacts may also be delayed as time is taken for local populations to reach critical life-stages where fine sediment limits survival.

CONTROLS ON SEDIMENT YIELD AND DELIVERY TO THE RIVER CHANNEL

The yield of fine sediment to the river channel from the catchment (expressed as specific yield, $t\ km^{-2}\ yr^{-1}$) is a consequence of the mobilisation of sediment from a variety of sources, the transport of that sediment through the landscape and any storage, either temporary or longer-term, within the landscape. Hence, many factors influence the quantity and composition (including *inter alia* grain size, organic content, and associated contaminants and nutrients) of fine sediment delivered to the channel. Whilst soil type, climate and geology have a major influence on the mobilisation of fine sediment, their effects are modified by local factors, including topography, land-use, vegetation and management. As the mobilised fine sediment is transported through the landscape from the source to the river, there is further potential for sorting and retention to influence the quantity and composition of the sediment ultimately delivered to the river channel. For this reason, well-connected sources tend to contribute most to the fine sediment yield.

As the characteristics of sediment from different locations and sources vary (e.g. arable land, road verges), methods have been developed to identify and apportion the contributions from the various potential sources of both the inorganic (e.g.[12,13]) and organic (e.g.[14]) components of fine sediment sampled from rivers. Such source apportionment studies indicate that some sources contribute disproportionately relative to their area in the catchment, particularly those that are well-connected, either arising close to the river or involving pathways over impervious surfaces, or both (e.g. direct inputs from sewage treatment works, damaged road verges)[14–16]. Part of the yield is derived from natural processes such as unenhanced background erosion of soils and river banks. However, the dominance of human influences on the landscape has affected fine sediment dynamics since early agriculture[17–19]. More recently, the total yield of fine sediment has increased from historical levels, particularly in the post-war years with the intensification of agriculture and expansion of urban areas[20], such that agricultural, industrial and urban sources now contribute a substantial proportion, if not the majority of the yield of fine sediment to rivers[2]. As such, both the quantity and composition of fine (inorganic and organic) sediment delivered to rivers far exceeds modern background levels; the estimated total loss of sediment in England and Wales was 1,389,818 t yr-1 in excess of target modern background delivery rates[21], defined as the early twentieth century up to ~1940[20]. ~~(defined as the early twentieth century up to ~1940)[20,21].~~

ABIOTIC CONTROLS ON FINE SEDIMENT TRANSPORT AND STORAGE

Controls on fine sediment: Hydraulics and geomorphology

Transport and storage of fines in streambeds plays a key role in the natural development of the sediment matrix[22–24], contributing to habitat quality and quantity by influencing the hydrological and geomorphological behaviour of a river[25]. Fine sediments are composed of organic and inorganic components that are transported in rivers as solid load or may precipitate from the dissolved load ($<0.45\ \mu$m). The majority of fines move through river systems as solid suspended load[26] in the form of flocculated or aggregated particles due to their cohesive nature[27]. The load of fine sediments in a river will be determined by the relationship between flow conditions and the structure, density and size of the sediment particles.

The magnitude and timing of events exhibiting high suspended sediment loads ~~is~~ are closely related to the hydrological regime. In rivers with a near-natural flow regime, sediment transport is positively correlated with flow intensity[28]. Human alterations, such as dams and channelisation, that modify or disrupt the flow and sediment longitudinal continuity, have multiple effects on sediment dynamics and the morphology of downstream reaches[29]. Moreover, sediment flushing operations adopted for the maintenance of reservoirs can lead to extreme events characterised by high suspended sediment loads and the potential for widespread deposition downstream[30].

Most accumulation of fines in the streambed occurs as a result of gravitational deposition from the suspended load[5,22,23,31–33]. Hydraulic conditions in the water column determine whether such deposited fines are stored on the bed surface, resuspended[34], or infiltrated into the bed[11]. Pressure gradients at the bed sediment-water interface[35,36] may promote suspended sediment advection into the porous matrix via downwelling and upwelling mechanisms[23,33,37,38]. Such pressure gradients are induced by bedforms[35,39], local heterogeneity or roughness and permeability changes in the streambed[40], including those created by biotic activity. Fines infiltrating into the streambed may settle within the pore spaces of the sediment matrix[41], or be transported laterally and longitudinally through the streambed[42]. In the upper bed layers, such horizontal transport (‘Brinkman load’ in Figure 2) may result from turbulent mixing promoted by shear instability above the bed[5,43,44]. In the lower layers, subsurface (Darcian) flow driven by hydraulic gradients[45] may transport fines through the interstitial spaces of the sediment matrix[44] (‘interstitial load’ in Figure 2).

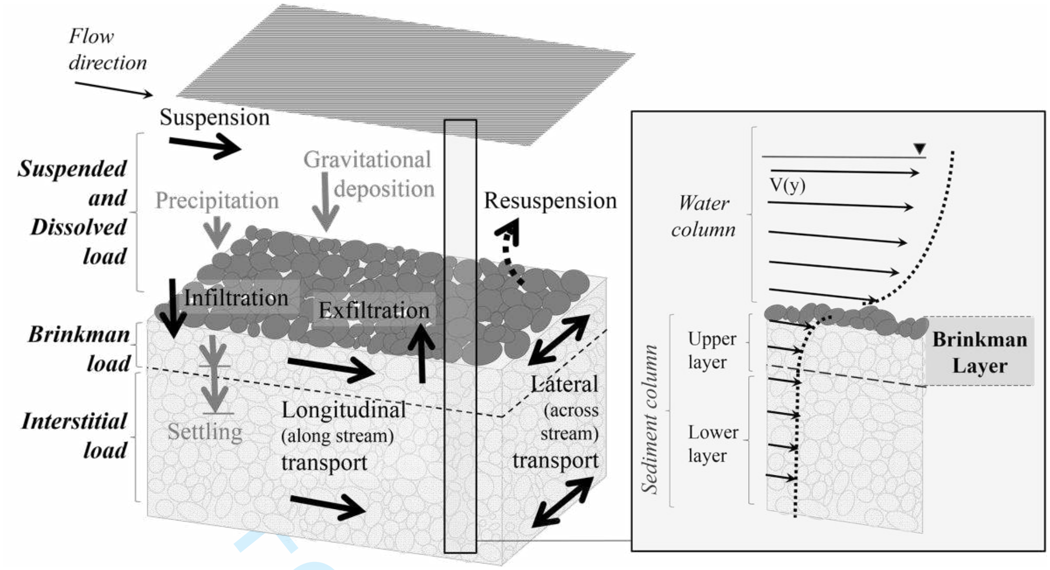


Figure 2 - Fine sediment transport (black arrows) and deposition (grey arrows) processes in gravel beds. These processes occur in three key load regions (suspended and dissolved load, Brinkman load and interstitial load) within the water and sediment columns in which such processes occur (left). The model proposes distinct modes of sediment transport in these three regions identified by transitions in the velocity profile V(y) (right). Modified from[44].

Controls on fine sediment: Physico-chem~~s~~istry

The physico-chemical properties of fines are typically considered to be secondary in importance to their physical characteristics in terms of generating ecological impacts, yet there are clear feedbacks between the sediment, its chemical constituents and those of the water-column, and biotic activity. Indeed, the chemical composition of fine sediment may be more influential on invertebrate assemblage structure[3,46,47] and the survival of fish eggs[48,49] than the volume of fines deposited on the benthos[50]. However, it is generally acknowledged that combined multiple stressor effects are complex and poorly understood[51,52]. Some of the better understood feedbacks between the physico-chemical properties of fines and their dynamics are related to biological processes. For example, the scattering and prevention of solar radiation by turbid conditions caused by excess suspended sediment is known to be detrimental to benthic ecology by reducing rates of photosynthesis[53,54]. Similarly, high suspended sediment concentrations (SSC) drive temperature gradients with depth in the water column[55], with consequences for biotic activity. Another well-studied impact on the benthic community is a reduction in hyporheic exchange flow due to the deposition of excess fine sediment[11,56]. Within the interstices, the breakdown of fine particulate organic matter (FPOM) increases sediment oxygen demand, exacerbating the hypoxia initiated by physical clogging[49,57–60]. Under such conditions, methanogenic microbial communities develop at the oxic-anoxic interface, resulting in the precipitation of ocherous masses of iron hydroxides[61] and further saturating the bed matrix with fine particulate matter.

Many of the direct physico-chemical impacts of fines on stream biota are ecotoxicological in nature, driving feedbacks by increasing or decreasing the biological controls exerted on fine sediment dynamics

(Figure 1). Nutrients, heavy metals and organic pollutants can adsorb to and desorb from fine particles due to their high affinity as carriers[25,62,63]. Their sorption potential depends upon the properties of the sediment, i.e. grain size, mineralogical composition, organic matter content and cation exchange capacity[64]. The physico-chemical weathering of sediments during their 'life-cycle' is driven by water column concentrations of major ions and trace chemical constituents[65], in addition to biological and hydrodynamic processing and sorting. However, additional physico-chemical factors, such as dissolved oxygen, pH and temperature have also been implicated in controlling the sorption dynamics of potentially harmful substances, including heavy metals[66] and nutrients[67].

The desorption of these substances may increase bioavailability, allowing contaminants to enter the food web along with those contaminants adsorbed to fines that are ingested by biota. For example, the exchange of various phosphorus (P) forms between the particulate (bound) and dissolved (free) pools within freshwaters is now well-documented to be influenced by pH, temperature and dissolved oxygen[68]. These interactions can either promote or inhibit growth depending on the stoichiometric abundance of nutrients or the toxicity of contaminants[69–71]. Other physico-chemical factors affecting fines may disrupt their transport and deposition mechanics. An increase in the deposition of fines due to flocculation and precipitation has been seen due to modification of pH and ionic salt concentrations in freshwaters[72–74]. The most widely known examples are changes in redox potential leading to the deposition of calcium salts (tufa) and ocherous masses. Temperature regulated ~~stream~~water viscosity is also known to increase particulate deposition[75]. These physico-chemical feedbacks between fines, the water-column and biotic activity have complex, cascading effects on geomorphic processes.

~~BIOLOGICAL~~ BIOTIC CONTROLS ON FINE SEDIMENT TRANSPORT AND STORAGE

The two-way interactions between biota and the environment have long been of interest to both physical and biological scientists. However, it was not until recent decades that they were more intensively investigated under a multitude of frameworks, including zoogeomorphology, ecogeomorphology, biogeomorphology and ecosystem engineering[76–78]. Below we briefly review the body of research that has emerged from application of these frameworks to biofilms, aquatic macrophytes and riparian vegetation, invertebrates and fish. In doing so, we highlight the key *effect* traits[79] that determine the potential of biota to influence fine sediment dynamics (Table 1).

Controls on fine sediment: Biofilms

Biofilms, referred to as 'cities of microbes'[80,81] comprising bacteria, fungi and algae[82], are known to affect and be affected by fine sediment dynamics[83–86]. Although the important function biofilms fulfil in wastewater processing has long been known, it was not until more recently that research began to focus on their role in the processing and fate of fine sediment-bound contaminants in freshwater ecosystems[87–91]. The matrix of the biofilm microenvironment is comprised mostly of extracellular polymeric substances (EPS)~~EPS~~[92,93], which are synthesised by the biofilm microbial community. The properties of these EPS are influential on the sediments upon which they establish, altering their physico-chemical characteristics and, therefore, their dynamics through bioflocculation[94]. An experimental study[95] found that the erodibility and resulting resuspension of settled cohesive sediments was reduced with weak biofilm EPS growth when exposed to low shear stress (<0.1 Pa). Longer periods (up to 12 days) of undisturbed growth under low shear stresses (<0.1 Pa) allowed the establishment of a biofilm-EPS structure that could reduce erosion under increased shear stresses of up to 0.4 Pa. These results, along with other studies in agreement[85,96,97], demonstrate that biofilm growth and the corresponding EPS synthesis allows for increased cohesion between fine sediment grains (Figure 3). This potentially increases the deposition of fines and reduces their resuspension[98].

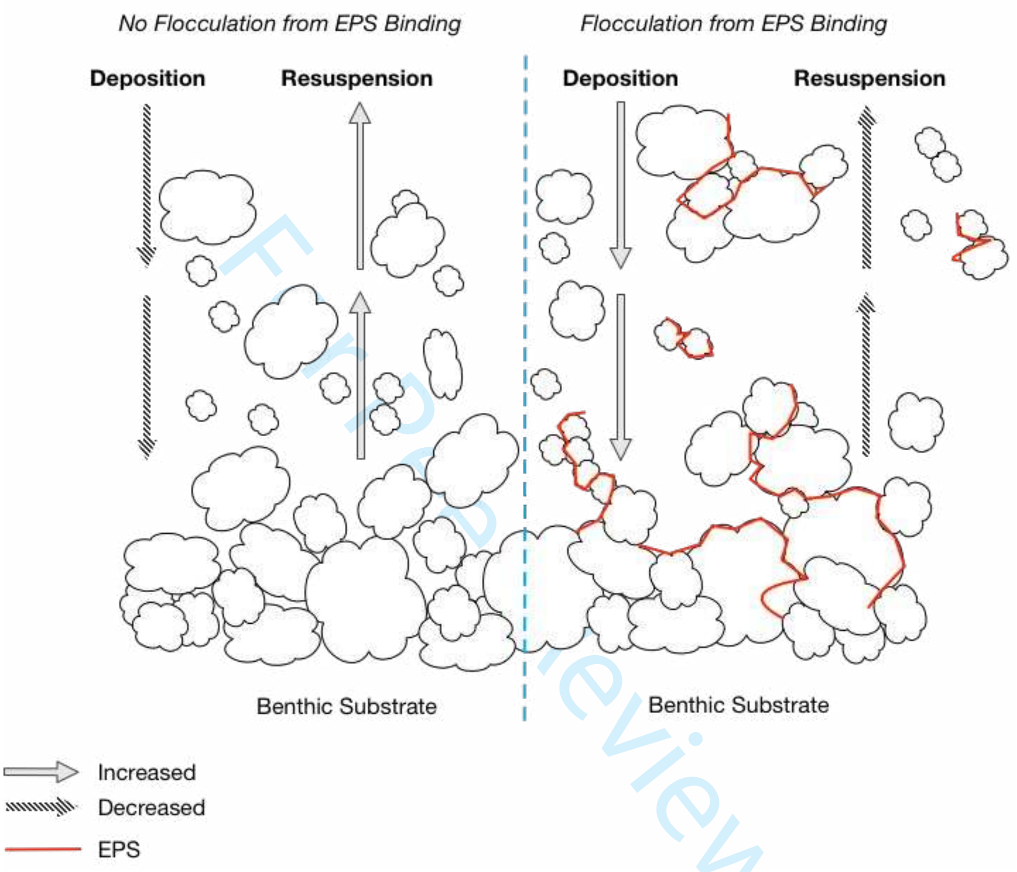


Figure 3 - Controls on fine sediment deposition and resuspension exerted through bioflocculation by extracellular polymeric substances (EPS) in biofilms.

Fine sediments also interact with sediment-water exchanges of nutrients associated with biofilm communities[27], typically increasing community growth and EPS synthesis. During a flume study[87], concentrations of soluble reactive phosphorus (SRP) were reduced through the trapping of fine particulates in biofilms. Bed sediments with larger surface areas for biofilm and filamentous algal growth resulted in a greater flux of SRP than fine sediments alone, which are unable to support filamentous growth. Furthermore, evidence that nutrient stoichiometry is influenced by fine sediment dynamics has been linked to changes in biofilm growth and species composition[99,100]; although it is acknowledged that physico-chemical factors also play a role[101–103]. The growth of biofilms has also been found to influence fine sediment transport and bed morphology[85,104]. Modelling following experimental observations has demonstrated that biofilm-coated fines have a greater saltation length-height ratio, suggesting that particle deposition and settling is more likely than in uncoated fines, depending on water velocity[105]. More recently, a microbiological-physical model (BFLOC2) of suspended sediment aggregation and settling velocity was established[106]. The model shows that microbial biomass, cell motility and aggregate-attached food web interactions are significant controls on fine sediment dynamics. In summary, the interactions between biofilms and fine sediments are driven by a balance between physico-chemical and biotic influences on the processing, transport and fate of particles.

Controls on fine sediment: Macrophytes and riparian vegetation

Awareness of the intimate links been vegetation and river landforms and processes emerged during the last century [107–109]. However, recognition of the complex interactions between riparian vegetation and fluvial processes that result in sediment retention and landform building has only emerged strongly in the last two decades[110–112]. It is now recognised that particular plant types, materials and species are key to these interactions, driving meso- to macro- scale sediment retention and building landforms. Examples of the broad types of plants and plant-derived material include emergent[113,114] and submerged[115] aquatic macrophytes; dead[116] and living deposited trees[117,118], tree fragments[119] and accumulations of fragments[120].

Interactions between plants and any fine sediment transported by rivers are particularly important because small sediment particles are easily mobilised, even at low flow velocities, and so their storage relies on them being retained in sheltered locations. The above-ground biomass of plants offers such shelter to exert control on fine sediment retention. The extent to which plants drive such retention is dependent on their ability to affect local hydraulic conditions, and hence their morphology and the stiffness and density of their stems[9]. The greater the resistance the plant presents to flow, the greater the retention of sediment[121,122]. Once a critical flow resistance (frontal area drag coefficient) has been achieved, plants will tend to retain sediment[123]. Aquatic plants have the ability to grow through the retained sediment, reinforcing it with their stems, roots, rhizomes and other below-ground organs and driving the further accumulation of fine sediment into erosion-resistant, aggrading landforms such as bars, benches, river banks, islands and floodplains[124]. In lower energy river systems, aquatic macrophytes may be more important as ecosystem engineers than riparian plants [9,121,125]. For example, the emergent macrophyte *Sparganium erectum* is a very effective river ecosystem engineer in British lowland rivers[126]. A beneficial effect of sediment retention by plants can be that, as the fine sediment landforms emerge from the ~~river bed~~streambed, they narrow the width of river channel available for water, leading to increased flow velocities in the area occupied by water and thus increased transport and (re)mobilisation of fine sediment from any coarser bed material. The result is a more heterogeneous ~~river bed~~streambed supporting patches of contrasting particle size. Conversely, extreme macrophyte growth in dense stands may reduce flow velocities throughout the river channel, causing more sediment retention and homogenisation of the physical habitat[127]. This process could eventually lead to infilling of the channel. Indeed, it could be argued that such circumstances often arise as a response to the artificial creation or enlargement of stream channels, flow regulation and/or excessive inputs of fine sediment. Whatever the cause, available stream power is insufficient to control macrophyte growth and flush fine sediments[114,128]. ~~Regardless of the cause~~In any case, the fine sediments retained by macrophytes frequently display a high organic content[129], illustrating that this interaction between plants, fluvial processes and river morphology may have a notable role in organic matter retention. Such effects are likely to be more pronounced in nutrient-enriched waters.

As river energy increases, macrophytes are unable to resist the increasing shear stresses imposed by river flows, and their engineering role is taken up by riparian plants, particularly trees. All tree species growing along river margins interact with fluvial forms and processes through a 'large wood cycle'. Tree or branch fall introduces large pieces of wood into rivers, where they can snag and accumulate into wood jams or dams, providing retention structures for other organic material, sediments and seeds[116]. In unmanaged situations, these processes drive a cycle of sediment and seed retention, germination and growth, and incorporation of the aggrading vegetated landforms into islands and floodplains where they support the growth of trees and thus the delivery of more large wood to the river[130]. Across the temperate zone of the Northern Hemisphere, the Salicaceae (willows and poplars) are particularly important river ecosystem engineers[131]. Riparian species of willow and poplar not only drive a 'dead' wood cycle, as described above, but the ability of wood from these species to sprout and grow remarkably rapidly, makes them particularly effective river ecosystem engineers. Furthermore, these species can produce roots from buried stems and shoots from roots allowing them to strongly reinforce sediments to depths of several metres[132–134].

Recent reviews[124,135] conceptualise the crucial interactions between plants and fluvial processes that influence sediment retention and reinforcement, the building of landforms such as scroll bars[136], islands, river banks and floodplains that are the result of these interactions, and the ways in which these processes and forms vary through time and across space. During the storage period in these landforms, the properties of fine sediments may change under the influence of biogeochemical processes and the activities other biota that colonise the new landforms. This could include invasive species, such as the tall growing annual Himalayan balsam (*Impatiens glandulifera*) which may increase the risk of bank erosion during the winter period[137,138]. The controls on fine sediment transport and storage exerted by plants, therefore, may be shifting as invasive species become established.

Controls on fine sediment: Invertebrates

Lotic invertebrates are key ecosystem engineers, being ubiquitous in rivers and often present at considerable densities. For this reason, despite their typically small body sizes (e.g. <50 mm), invertebrates can have substantial cumulative impacts on the storage and transport of fines[139]. Crustaceans are perhaps the most widely studied geomorphic agents in rivers and can influence all aspects of fine sediment dynamics[140]. Crayfish can destabilise ~~river beds~~streambeds during activities such as foraging and fighting, and a number of studies have documented an increase in turbidity attributed to bioturbation by crayfish[140,141]. High densities of invasive ~~The presence of~~ crayfish can result in a 50-75% reduction in the shear stress required to entrain sand, leading to increases in sediment fluxes of as much as 32%[142]. Invasive signal crayfish (*Pacifastacus leniusculus*) can also enhance the delivery of fine sediment to rivers through increasing bank erosion with high densities of burrows (up to 14 burrows m^{-1})[142,143].

Aquatic insects can increase the suspension of fine sediment by winnowing it from interstitial spaces during foraging activity[144,145]. The stonefly ~~(~~*Dinocras cephalotes*~~)~~ has the potential to erode 200-400 kg m^{-2} yr^{-1} of sand, with reduced prey availability increasing rates of sand erosion[146]. The mayfly species *Pseudiron centralis* manipulates near-bed hydraulics to disturb sand and facilitate capture of its prey[147]. This latter example demonstrates that some invertebrates are actively seeking to control sediment dynamics, an instance of extended phenotype engineering, whereby organisms create structures that directly influence their fitness and survival[78]. Invertebrate bioturbation has also been documented to influence sediment structure. Upward conveyors (Oligochaeta) and gallery-diffusers (Chironomidae) can reduce the clogging of ~~bed sediments~~streambeds, helping to restore hyporheic exchange flow and physiochemical conditions at the surface-subsurface interface[148–153]. Molluscs have been reported to both disturb sediment during movement and consolidate it whilst stationary[154]. Flow resistance generated by the shells of bivalve molluscs can also promote localised scour[155]. Different modes of bioturbation (sediment reworking, biogenic structure building, burrowing depth, bioirrigation) can also determine the impact of benthic invertebrates on microbial activities and biogeochemical processes in the sediment[156].

Hydropsychidae is one of the most abundant families of lotic insects worldwide, often accounting for as much as 80% of invertebrate biomass in some streams and, consequently, exerting substantial controls on geomorphic processes[157–159]. Hydropsychids construct nets to filter FPOM from the water column, increasing the force required to entrain bed sediments by 10-30%[142,160]. This effect increases with the density of individuals and the local richness of species exhibiting similar behaviours[161]. Through net-spinning, hydropsychid caddisflies increase the force required to erode armour layers and therefore reduce exposure of underlying fine sediments to entraining flows[162]. Many other species of caddisfly are also known for their construction of cases from mineral and organic sediment. These cases utilise a wide range of particle sizes and may be responsible for the ~~storage of significant quantities of~~ temporary storage of fine sediment[163,164]. Blackflies (Simuliidae), bivalve molluscs and other filter feeding invertebrates are also involved in driving storage of fine sediment by consolidating suspended particles from the water into faeces or pseudofaeces, thus increasing the rate of sedimentation and altering the composition of suspended solids[165,166].

The sheer diversity of aquatic invertebrate species (85% of global freshwater animal diversity[167]), and the densities in which they are often present, complicate understanding of their role in the transport of fines. In particular, interactions between coexisting species probably play an important role in mediating the impacts of excess fine sediment, yet these interactions are rarely considered[161]. It should also be noted that the effect of biota on fine sediment dynamics will vary spatially and temporally. ~~Four main factors have been suggested as primary controls on the impact that animals have on the environment; behaviour, body size, density and abiotic context[165,166].~~ Despite management advances made in recent decades, especially in relation to organic pollution, freshwater biota face increasing challenges for survival, including habitat degradation, species invasions, pollution, climate change, and increasing urbanisation[168,169]. Invertebrates are one of the most affected taxonomic groups[170,171] and this could have consequences, not just for biodiversity, but also fine sediment dynamics in the future.

Controls on fine sediment: Fish

Fish can exert controls on fine sediment dynamics through a number of activities. Relative to other taxonomic groups, the controls exerted by fish are well-documented~~, most notably feeding and spawning~~[140]~~.~~ . We therefore provide only a brief summary here. To date, salmonid spawning has attracted the most attention. During spawning, female salmon create redds (nests) by disturbing the bed with strong undulations of their tails[172]. This activity leads to the suspension of fines and modifies bed stability by vertically mixing gravels and fine sediments and disturbing existing armour layers[173–175]. Tail slips (material excavated from redds) are particularly vulnerable to scour[175,176]. Spawning salmon substantially modify topography across large areas of the bed[177]. This effect persists until the next high flow event of sufficient magnitude[178], exerting a strong, temporary control on the hydraulic processes driving fine sediment dynamics.

Put into perspective, the spawning activities of salmon and other lithophilous fish can have considerable geomorphic impacts at large spatial scales. The vertical mixing of material by salmon may be at a comparable magnitude to that driven by floods, resulting in lower critical shear stresses required to initiate bed movement[179]. In some cases, salmon can be responsible for a substantial proportion of annual sediment transport. A study in British Columbia ~~study~~ estimated that salmon account for one third to one half of total annual sediment flux in gravel bed streams[178]. So strong is this effect that the ~~evolution~~ evolution of freshwater fish may~~of multiple Pacific salmon species from a common ancestor may have consequences for landscape evolution over geological timescales~~profoundly influence channel erosion processes and stream profiles over geological timescales, as suggested by a coupled biological-landscape evolution model focusing on the descent of Pacific salmon species from a common ancestor[180].

Benthivorous fish also have significant impacts on fine sediment suspension while foraging. Cyprinid species can substantially alter sediment dynamics, increasing mixing depth and ~~suspended sediment~~SSC[181,182]. Foraging barbel, for example, can increase total sediment yields by as much as 82%[183]. The geomorphic impacts of benthivorous foraging increase with fish density[184–187], with the body size and mass of individuals[188], and with the presence of specific feeding behaviours. European barbel (*Barbus barbus*), for example, feed in both gravel and sand sized substrates, while gudgeon (*Gobio gobio*) feed largely in sand habitats and, therefore, their geomorphic impacts are spatially limited[189]. Fish can also exert controls on fine sediment dynamics indirectly through their influence on other biogeomorphic agents. For example, bed disturbance and predation by fish may reduce the controls exerted by net-spinning caddisflies, macrophytes and algae[189]. Moreover, fish can have considerable impacts on the biogeochemical processes in rivers~~,~~. For example, spawning migrations of anadromous fish (e.g. *Oncorhynchus* spp.) ~~may be~~can be a~~ potential~~n important source of marine-derived nitrogen and phosphorus to nutrient~~-~~-poor habitats[190,191], profoundly influencing the structure and function of ~~further influencing aquatic and riparian biota~~aquatic and terrestrial ecosystems[185].

CONTROLS ON ECOLOGICAL RESPONSES TO FINE SEDIMENT

Whilst the impacts of excess fines on biota can be pervasive[7–10] not all communities will be equally sensitive. In particular, the functional traits of the local biotic community, as well as those of the species comprising the regional species pool, will constrain the ecological response. Response traits determine an individual's ability to survive in different environmental conditions through characteristics that promote resistance and resilience to disturbances. Typically, such traits include information on morphology, phenology, behaviour and resource use[192,193]. Below we identify some of the major traits that are commonly associated with responses to fines (Table 1) and put them into context with biogeographic processes.

Table 1 - Traits involved in the effect of biota on fine sediment dynamics and the response of biota to excess fine sediment.

Taxonomic group	**Effect traits**	**Response traits**
All biota		- Dispersal capacity
Biofilms	- Extracellular polymeric substance (EPS) production - Colony structure - Growth rate	- Colony structure - Motility - Size and shape - Cell wall structure (rigidity) - Photosynthetic capacity
Plants	- Shoot density - Shoot and root structure - Shoot flexibility	- Fecundity - Asexual (vegetative) reproduction - Dispersal mode (hydrochory, anemochory) - Reproductive timing - Growth rate - Shoot flexibility in high-flow periods - Root structure and binding capacity
Invertebrates	- Feeding behaviour - Burrowing activity - Construction of feeding and protective structures (e.g. nets, cases) - Body size	- Feeding mode and diet - Body size and shape - Respiration mode - Locomotion (e.g. burrowing, crawling) - Reproduction mode (e.g. parental care, oviviparity) - Reproductive timing - Voltinism (number of generations per year)

Fish	- Foraging behaviour - Diet - Spawning behaviour	- Trophic guild - Foraging behaviour - Gill morphology and physiology (e.g. increased mucus secretion, gill epithelium thickness) - Mechanosensory system development (e.g. vision, lateral line) - Reproductive timing - Spawning behaviour

Controls on ecological responses: Biogeography

In rivers, the spatial distribution of organisms is highly dependent on the dendritic network structure[194]. Thus, at a broad level, ecological responses to fine sediment depend on the location of the site under consideration, as well as the topology and connectivity of the whole network[195]. The responses will also depend on the spatial structure of populations present within the network; if a population can be divided into subpopulations connected via dispersal, we may call it a 'metapopulation'[196]. 'Metacommunity' theory extends this idea to the community level by incorporating the effects of species sorting ('environmental filtering'[197]) and biotic interactions[198]. The theory, as applied to river networks, predicts systematic variation in the forces driving community assembly with stream order (Figure 4). All else being equal, the impacts of stressors such as fine sediment are predicted to reduce alpha diversity in headwaters, where colonisation of ~~adapted~~ species and phenotypes adapted to stress caused by excess fine sediment is limited. Mid-basin locations, on the other hand, are expected to exhibit high rates of turnover in species composition, as efficient species sorting leads to rapid selection of adapted taxa from the species pool. Further downstream, the effects of the stressor are predicted to be dampened by the influx of organisms from upstream, to some extent regardless of the environment. Superimposed onto this trend is a natural tendency for the importance of fine particulate matter as a basal resource to increase downstream through the river network[199]. Fine sediment storage dynamics in high order river-floodplain systems are also tightly linked to flood pulses that are relatively predictable compared to events in low order streams[200]. These spatial patterns are further complicated by the discontinuities in fluxes of matter and energy caused by riverine barriers such as dams[201].

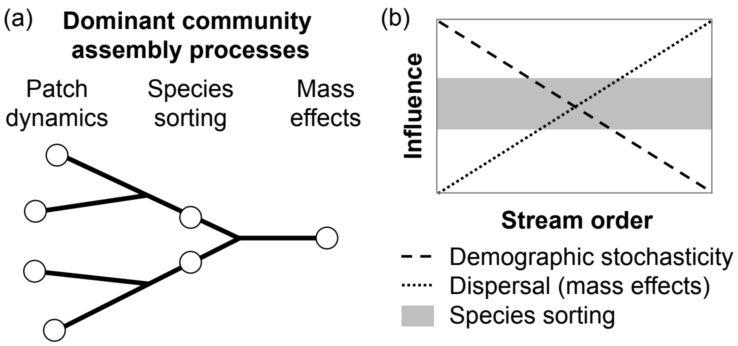


Figure 4 - Metacommunity theory predicts patterns in dominant community assembly processes in river networks (a) due to variation in spatial, environmental and demographic influences with stream order (b), with implications for ecosystem responses to stressors. Headwater communities are likely to follow the patch dynamics paradigm, whereby local species diversity is limited by dispersal and community structure becomes a function of stochastic demographic processes involving local extinction and colonisation[198]. The structure of lower mainstem communities is predicted to more closely resemble the regional species pool since high dispersal rates drown out the influence of the local environment through 'mass effects'[198]. In mid-basin locations, species sorting or 'environmental filtering'[197] is made possible as the influence of dispersal is at an optimal level to allow for efficient niche-based processes[202].

Whilst metacommunity theory provides a useful lens with which to study ecological responses to stressors, there are other regional-scale factors involved. Among these are biogeographical factors linked to the size of the species pool[203]. Relative to the number of taxa found at a given site, larger species pools are likely to contain species better adapted to a given stressor. Sites that are more saturated with respect to the species pool, on the other hand, will have less potential for adaptation. In the former case, high rates of turnover would be expected, whereas in the saturated case greater reductions in alpha (local) diversity are likely to ensue. These tendencies are further dependent on the traits expressed by taxa in the local assemblage and the wider species pool. In particular, the dispersal capacities of the regional fauna will, to a large extent, influence the relationship between the species pool, the local assemblage and stressor-driven changes[204]. In general, a weaker dispersing taxon will be less likely to colonise a newly suitable habitat patch after some environmental change, the likelihood also being contingent on the distance of established populations of that taxon from the impacted site[205]. Species pools are thus best represented as species- and site- specific probabilistic functions[206]. We consider other important traits controlling ecological responses below.

Controls on ecological responses: Biofilm traits

Biofilms comprise a mixture of heterotrophic (e.g. fungi, bacteria, protozoa) and autotrophic (e.g. cyanobacteria, algae, chemosynthetic bacteria) organisms, with many of the latter highly dependent on light. As such, the attenuation of light caused by increased sediment loads (either suspended or deposited) adversely affects the photosynthetic component of biofilms[207], shifting the balance of these two traits, and thus the net primary production of affected biofilms[208–211]. For the sessile photosynthetic components, the absence of light caused by burial beneath depositing sediment can be catastrophic and the only option can be to produce resting stages to endure the period until erosion brings them to the surface once more. However, for motile taxa (e.g. raphid diatoms, ciliates, flagellates) shading from deposited fine sediment may not present a substantial problem, as they can move to higher light intensities at the streambed surface[212,213]. Hence, diatom assemblages tend to become dominated by motile taxa where rates of deposition of fine sediments are high[214–216], although this trait (motility) may offer benefits under other conditions (e.g. nutrient rich conditions) such that the relationship with fine sediment is not straightforward[217].

The fact that deposited fine sediments are relatively unstable (compared with larger particles) renders them unsuitable for the attachment of long-lived sedentary species, particularly slow-growing and chain-forming taxa, pushing assemblages towards rapidly growing, single celled taxa. Whilst the lack of stability tends to result in reduced diatom taxon richness and biomass compared with more stable sediments[218,219], patch disturbance history has a large influence on the development of biofilm communities[220]. In turn, those taxa that exude mucilage are favoured, at least initially, as they tend to stabilise sediments (see discussion on EPS above).

The risk of being dislodged[221] or ~~suffering~~ undergoing physical damage[222] from suspended and particularly saltating sediment particles further selects against tall taxa (chain forming, filamentous, stalked and upright forms), and pushes communities towards adpressed forms and those that strongly adhere to the substrate (e.g. with mucilage pads), influencing traits associated with both growth form and attachment. More robust cell walls (e.g. thick walls, heavy silicification, costae) enable taxa to withstand physical damage. As such, species with thicker, more rigid cells walls are selected for where the suspended and saltating loads of inorganic sediment are high[223]. However, even these species are lost if disturbance is frequent[224]. Under more benign conditions, rapid growth rates may compensate for losses, with associated traits such as nutrient affinity being more apparent where deposited fine sediments are abundant[217].

Controls on ecological responses: Plant traits

River engineer plants possess important traits that allow them to establish and persist in riverine and riparian environments[9,225]. These traits include: (i) an ability to reproduce vegetatively, both to colonise new patches and to extend and consolidate patches once established; (ii) an ability to grow rapidly in order to maximise their chances of becoming established, and to cope with burial by deposited material; (iii) above-ground biomass with sufficient rigidity (either as individual shoots or collectively as stands) and stand density to present a resistance to flow and, thus, retain sediment, but avoids breakage under higher flows; and (iv) below-ground biomass with sufficient strength and appropriate architecture to anchor plants and resist uprooting (e.g. stolons, rhizomes).

Reproduction and dispersal traits allow plant propagules to reach appropriate sites for germination and establishment. Both aquatic macrophyte and riparian tree species take advantage of sexual and asexual means to ensure reproductive success, with different reproductive strategies allowing successful annual recruitment at different locations. However, riparian and aquatic engineer species generally devote considerable resources to asexual reproduction, in particular through the production of adventitious roots from stem fragments, allowing them to expand their cover locally as well as colonising new areas[226]. Asexual reproduction by riparian tree species largely depends on the ability of uprooted trees and wood fragments to sprout both roots and shoots once deposited. Some aquatic macrophyte species, particularly those with emergent growth forms (e.g. *Sparganium erectum, Glyceria maxima*), produce dense networks of rhizomes or stolons that support the spread of patches, as well as dispersal if the plant is fragmented, whilst others regenerate freely from stem fragments[227]. The development of adventitious roots, stolons and rhizomes allows plants to cope with burial and to consolidate the deposited material (e.g. [126]). Many aquatic plants and riparian shrubs (e.g. Salicaceae) develop such structures, which enter and reinforce aggrading sediments while maintaining reinforcement and erosion resistance in buried substrates (e.g. [132]). Furthermore, plants can exploit the nutrients available from deposited material by rooting into it: much of the organic material deposited in stands of *Ranunculus penicillatus* is remineralised and used for growth of the plant, further accentuating deposition[228], a characteristic likely to be true of other species.

Once deposited, propagules of engineer plants germinate or sprout and typically grow rapidly to anchor themselves and support their survival in disturbed river environments. Rapid shoot and root growth is particularly important for species both to exploit opportunities for growth before disturbance removes them and to cope with burial. For example, field observations along the Tagliamento River, Italy, have recorded main shoot growth in *Populus nigra*, *Salix alba* and *Salix eleagnos* seedlings, cuttings and from uprooted, deposited trees of up to 3 mm day^{-1}, 10 mm day^{-1} and 15 mm day^{-1}, respectively[229,230]. Furthermore, greenhouse experiments on cuttings of *Salix eleagnos* and *Populus nigra* have revealed vertical root penetration of 27 and 15 mm day^{-1} respectively for sand substrates, and 20 and 10 mm day^{-1}, respectively for gravel substrates under a water table falling at 30 mm day^{-1} [231]. Many aquatic plants avoid disturbance during winter and spring high flows by producing dense networks of rhizomes that persist through the winter, anchoring the plants and reinforcing penetrated sediments, whilst following an annual above-ground growth cycle whereby shoots emerge in the spring. Peak biomass is reached in mid to late summer and then senesce during autumn, leaving little (if any) above-ground biomass exposed during winter high flow events (e.g.[126,232,233]). During the growth period, species succession in aquatic plant stands is closely related to the ability to outpace the rate of deposition, favouring species with fast growth rates (including the ability to exploit nutrients from deposited material) and the capacity to adopt an emergent strategy[234,235].

As stated above, the extent to which plants retain sediment is related to the resistance they present to the flow of water. However, this resistance coupled with the instability of deposited sediment increases the likelihood of plants being uprooted, particularly during flood conditions. The prevalence of traits associated with rapid growth, either to cope with burial, patch instability or to exploit nutrients from deposited material, together with a high dependency on vegetative growth, leads to a plant trait syndrome similar to that seen in highly competitive taxa typical of nutrient rich conditions[236]. Hence, it is not surprising that taxa indicative of high nutrient conditions thrive in rivers with large amounts of deposited sediment[9,237].

Controls on ecological responses: Invertebrate traits

Excess fine sediment is widely acknowledged to have deleterious effects on the structure and function of invertebrate communities[8,54,60,238]. Substrates with a high volume of fines typically support homogenous communities that are dominated by relatively few taxa[47,239–241]. The composition of invertebrate taxa present in different environmental settings is strongly constrained by the functional traits they possess[242], resulting in variable tolerance or sensitivity to excess fines[243,244].

High sediment loads reduce the quality and availability of trophic resources which may reduce feeding efficiency, most notably for shredders[244–247]. Other feeding modes, including algal scrapers and filter feeders, also demonstrate some sensitivity to fine sediment[248–250] but the effect lacks consistency, suggesting that other factors interact with these traits to determine the response. Increasing infiltration of fines fills interstitial pore spaces and reduces dissolved oxygen concentrations, limiting the ability of many taxa to persist due to their body size, shape and respiratory requirements[251,252]. As such, streambeds subjected to high levels of deposition and infiltration are frequently characterised by taxa with small body sizes and lower densities of interstitial dwellers[60,246,253,254].

Locomotion traits may also be implicated in the impacts of fine sediment deposition on invertebrate communities. Burrowing taxa associated with depositional habitats are well adapted to fine sediment, whilst crawlers may be adversely affected during deposition events due to their reduced locomotive capacity[251,255–257]. Species with certain respiration modes can also be highly sensitive to fine sediment transported in the suspended or saltating load. Delicate gill structures, for example, may become physically abraded or clogged by fine sediment, limiting the exchange of oxygen[258,259]. Reproduction mode may also exert a strong control over which taxa are able to persist in substrates with high fine sediment content. Unattended eggs deposited onto the stream bed, for instance, may become smothered or abraded by fine sediment[260]. As a result, the prevalence of ovoviviparity, as found in diverse taxa (*e.g. Sphaerium spp., Asellus aquaticus, Cloëon spp.*), may increase in streams subjected to high sediment loads[246,261,262]. Voltinism also influences a taxon's ability to recover from distur~~ru~~bances such as those wrought by excess fine sediment, with mutivolitine taxa recovering more rapidly compared to univoltine taxa[257,263]. This resilience to disturbance is associated with a trait syndrome that includes small body sizes and short life cycle lengths.

Despite trait-based ecology gaining increasing recognition for its ability to predict tolerance and sensitivity to a range of stressors, further research is required to strengthen the mechanistic basis behind the use of invertebrate traits in fine sediment-specific biomonitoring applications[244]. The consideration of traits should be evaluated with caution as a number of recent studies have reported inconsistent responses of invertebrates to fine sediment deposition[47,246,254,257]. Traits are unlikely to act in isolation but rather as combinations of traits describing life-history strategies of varying resistance and resilience to stressors such as fine sediment[47,264]. Furthermore, the timing of fine sediment events relative to a taxon's life-cycle will play an important role[254] as will a taxon's preferred habitat and substrate composition[244].

Controls on ecological responses: Fish traits

A range of fish traits have been implicated in community responses to fine sediment carried in suspension, in the saltating load, surface deposited or infiltrated[7]. Well-documented, direct negative impacts include the clogging and abrasion of soft tissues, especially gills[265,266]. Fish adaptations to enhance resistance to this include increased mucus secretion and a thickening of the gill epithelium[267]. However, under high SSC, mucus secretions can result in increased susceptibility to clogging of the gill surface and ultimately suffocation of the fish[268]. Further adaptations to living in turbid conditions are associated with the mechanosensory system, including development of the lateral line system and inner ear used to sense hydrodynamic cues, specialised reflective structures in the eye, and tactile and olfactory senses[269–271].

By far the most well-known impact of deposited and infiltrated fine sediment is the smothering of salmon redds[49]. However, the majority of freshwater fish species are not lithophilous. Phytophilous species are also likely to be indirectly impacted due to reductions in submerged vegetation under high fine sediment loadings, whereas reproduction in psammophilous taxa may be favoured if deposition is associated mainly with the sand fraction. Some species avoid the potential impacts of fine sediment on eggs by ovipositing on riparian vegetation at high flows, with eggs developing out of the water until the next high flow (e.g. *Galaxias argentus*[272]). The timing of life-history events relative to periods of high fine sediment loadings can play an important role in fish responses to fines. In many temperate systems, for example, fine sediment accumulation in spawning gravels will likely be highest during the summer baseflow period[54]. Spawning outside of this period is therefore one way to avoid the most deleterious impacts on eggs and embryos[7].

Herbivorous fish are indirectly impacted by reductions in submerged macrophyte abundance and changes in plant species composition due to light attenuation and abrasive forces of suspended and saltating sediment, as well as the deposition of fine material on plant surfaces, which reduces plant growth and nutritional quality[9,273]. This generates further impacts on other species by reducing or changing the nature of available cover. Zooplankton feeders may benefit from enhanced foraging efficiency under high SSC as their prey congregate near the water surface[274], although the reduced visibility associated with such conditions is likely to result in net-negative impacts on feeding[275]. Similarly, high turbidity events may enhance prey availability due to increased invertebrate drift rates. However, foraging efficiency for drift-feeding fish decline under even mildly turbid conditions[276] and, in the long-term, invertebrate drift events in response to high SSC are likely to contribute to a change in invertebrate community composition which would negatively impact invertivorous fish[277].

Conclusion

The presence of excess fine sediment in rivers is a major reason for failure of EU member states to achieve Good Ecological Status under the Water Framework Directive. In this context, we have presented a broad synthesis of current understanding in the belief that this can help to drive the production of new scientific knowledge and inspire management innovation. In particular, we have highlighted biogeomorphic processes that control the transport and storage of fine sediment, and the mechanisms by which this elicits ecological responses and feedbacks. The fine sediment ‘problem’[11] represents a major challenge for applied environmental science worldwide but progress is being made towards a more complete understanding of the physical and biological processes involved. This progress should be maintained and accelerated by continuing the open dialogue between management agencies and scientists working within the broad disciplines of ecology, hydraulic engineering, fluvial geomorphology and hydrochemistry. In Sidebar 1, we briefly describe the outcomes of a workshop intended to address this need. Based on the experiences of environmental managers present, the workshop participants identified the most urgent knowledge gaps. These ranged from the collation of existing data and case studies to the investigation of responses to fine sediment at the population and whole ecosystem levels. ~~In this way~~Through initiatives such as this, key management challenges, scientific research priorities, and the production of new knowledge can all inform and shape one another ~~(see sidebar)~~.

SIDEBAR 1 - SUPPORTING GOOD ECOLOGICAL STATUS THROUGH RESEARCH

A British Ecological Society-funded workshop in July 2017 brought together early career researchers working on fine sediment internationally along with UK-based environmental managers and senior scientists in the field to discuss how to support the achievement of GES through research. The discussions indicated that fine sediment-related failures to achieve GES in England and Wales are largely due to agricultural and rural land management, followed by urbanisation and transport. Measures to address the problem for point and diffuse sources exist but there are gaps in the evidence, including information on the risk of further deterioration, impacts on protected areas, and the interaction of fine sediment with other pressures. More catchment-scale data is needed to inform management, along with greater collation of existing case studies. Evidence is required for the effectiveness of alternative measures under future climate change and socio-economic scenarios. Further development and testing of pressure-specific biomonitoring metrics will help to link ecological changes to causal factors.

Specifically, environmental managers needed answers to the following questions:

- What are sediment yields and dynamics in rivers under different land use and management scenarios?
- How do we define 'natural' sediment conditions in aquatic ecosystems?
- How much do we need to reduce the sediment input by to see an ecological benefit?
- How can we evaluate the benefits of reducing excess fine sediment in rivers?
- What are the impacts of invasive species on sediment regimes? – especially plants such as Himalayan balsam and burrowing animals such as crayfish.
- Are there thresholds of fine sediment loadings beyond which ecological impacts are more severe?
- How can the risks of fine sediment impacts on sensitive species, such as the pearl mussel~~s~~ (*Margaritifera margaritifera*), be assessed most effectively?
- Which management measures are most cost-effective?
- What are the risks of dispersive dredging from contaminated sediments?
- What is the role of fine sediment dynamics in the transport of microplastics?

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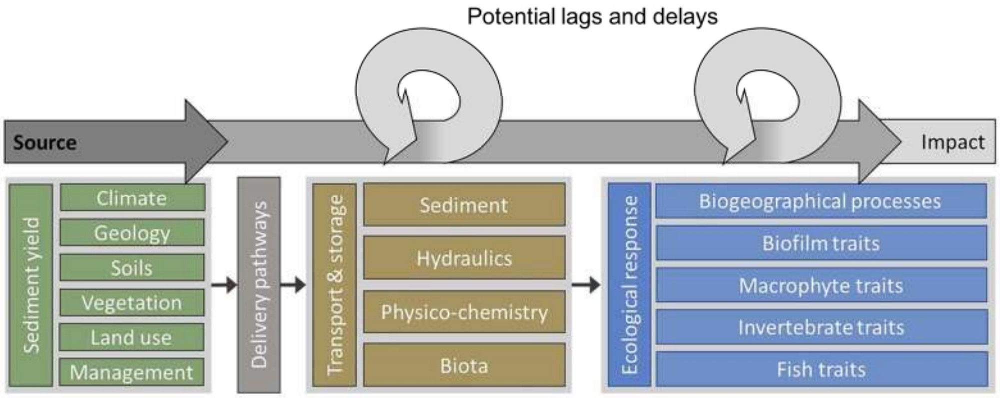
Further Reading

None. The bibliography is extensive.



114x46mm (300 x 300 DPI)

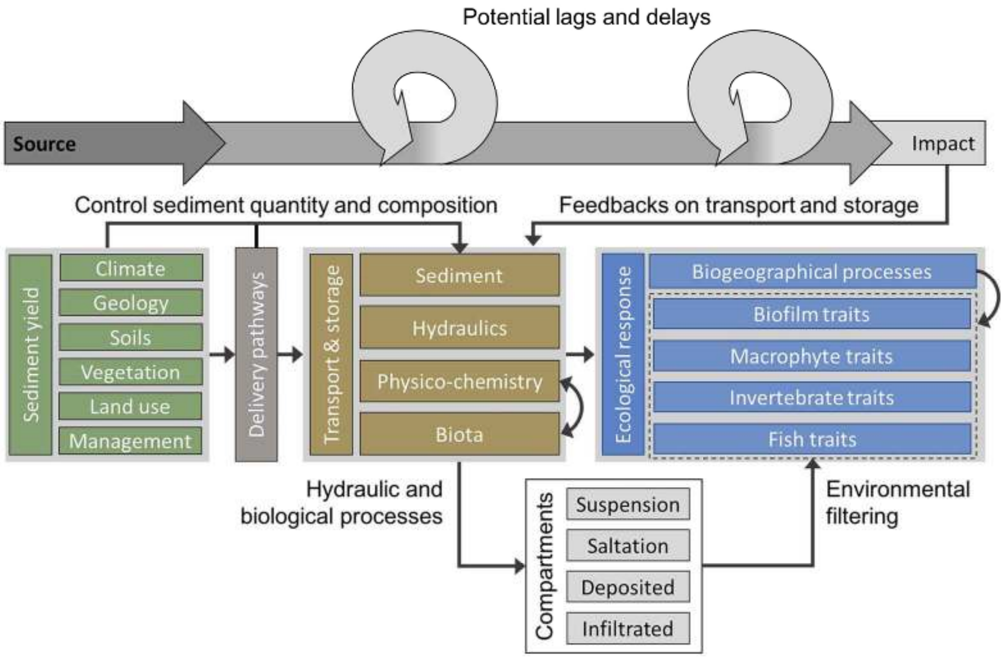


Figure 1 – Controls on the delivery, transport and storage of fine sediment and the resulting ecological responses in river networks. Natural and anthropogenic factors control the quantity and quality of sediment potentially available for delivery to the river channel. Whether or not this potential is realised, and the quantity and composition of sediment conserved during the pluvial phase, depends on delivery pathways that connect the source to the river channel. Once delivered to the river channel, particles may be transported through suspension or saltation, temporarily stored as surface-deposited material, or become infiltrated in the river bed and stored on a longer-term basis. Which compartment particles are transported or stored in depends on a number of controls, including the inherent properties of the particles, hydraulics, and the activities of biota. The latter is in turn influenced by physico-chemical factors (e.g. oxygen, nutrients) that work to limit or enhance biological processes. The hydraulic and biological controls determine the compartments within which particles are transported or stored, structuring the physical habitat, modifying available resources and potentially filtering out unsuitable species from the species pool on the basis of their traits. Such environmental filtering effects may be interfered with by biogeographical processes related to dispersal. The fate of fine sediment, and the extent and nature of the impact it causes is subject to potential lags as sediment is temporarily stored within the landscape. Ecological impacts may also be delayed as time is taken for local populations to reach critical life-stages where fine sediment limits survival.

188x124mm (300 x 300 DPI)

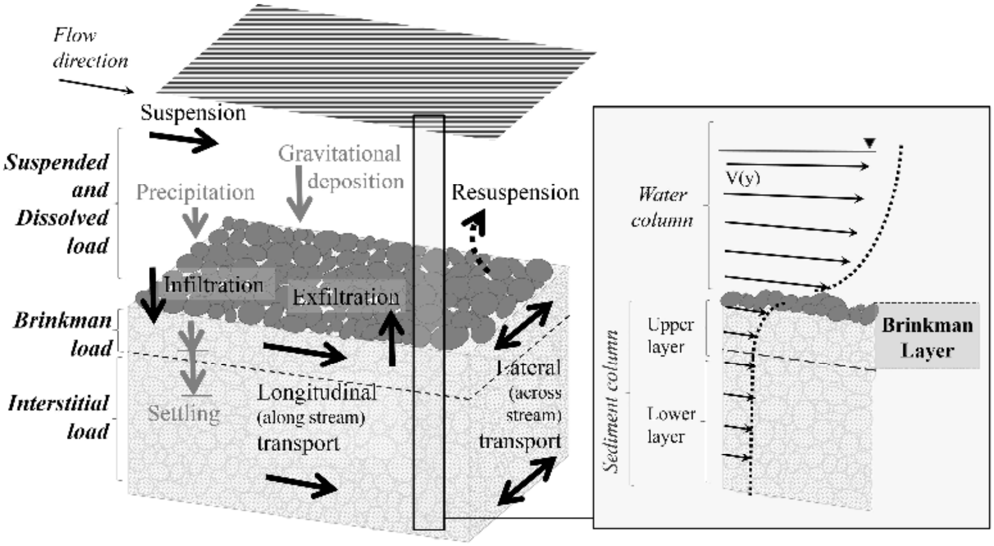


Figure 2 - Fine sediment transport (black arrows) and deposition (grey arrows) processes in gravel beds. These processes occur in three key load regions (suspended and dissolved load, Brinkman load and interstitial load) within the water and sediment columns in which such processes occur (left). The model proposes distinct modes of sediment transport in these three regions identified by transitions in the velocity profile V(y) (right). Modified from[43].

326x175mm (300 x 300 DPI)

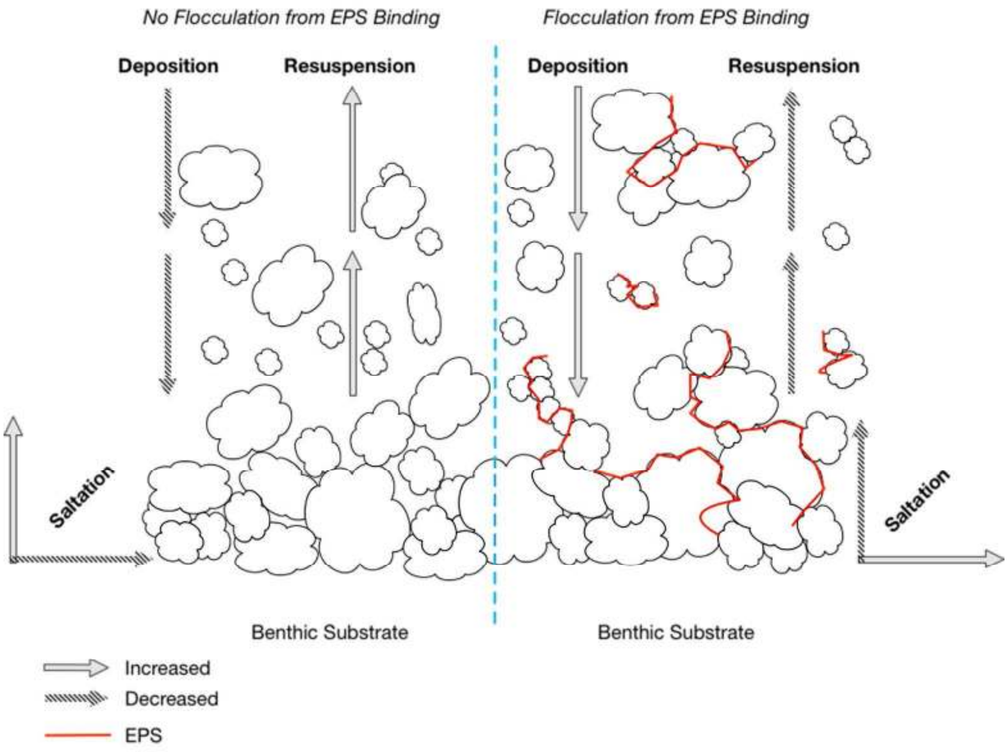


Figure 3 - Controls on fine sediment deposition and resuspension exerted through bioflocculation by extracellular polymeric substances (EPS) in biofilms.

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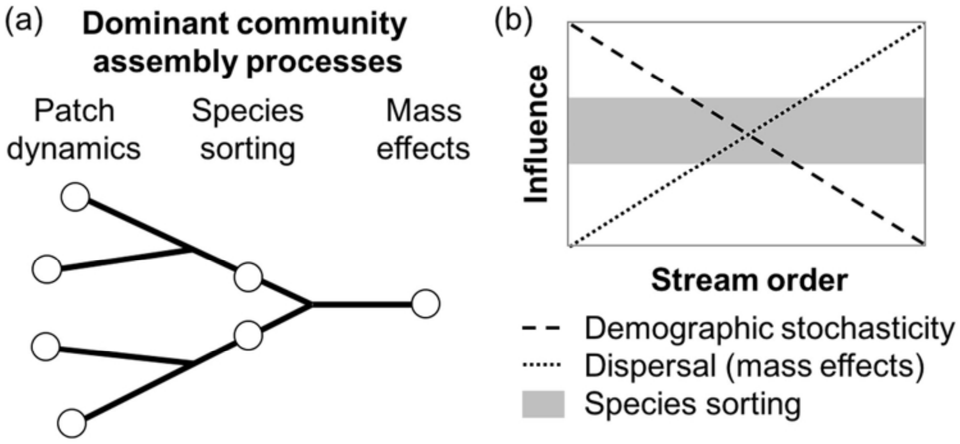

Figure 4 - Metacommunity theory predicts patterns in dominant community assembly processes in river networks (a) due to variation in spatial, environmental and demographic influences with stream order (b), with implications for ecosystem responses to stressors. Headwater communities are likely to follow the patch dynamics paradigm, whereby local species diversity is limited by dispersal and community structure becomes a function of stochastic demographic processes involving local extinction and colonisation195. The structure of lower mainstem communities is predicted to more closely resemble the regional species pool since high dispersal rates drown out the influence of local environment through ‘mass effects’195. In mid-basin locations, species sorting or ‘environmental filtering’194 is made possible as the influence of dispersal is at an optimal level to allow for efficient niche-based processes199.

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