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**Mason, R. and Sanders, H.**

# Invertebrate zoogeomorphology: A review and conceptual framework for rivers

Richard J. Mason<sup>1,2</sup>  | Harry Sanders<sup>1,3</sup> 

<sup>1</sup>Geography and Environment,  
Loughborough University,  
Loughborough, UK

<sup>2</sup>Department of Ecology and  
Environmental Sciences, Umeå  
University, Umeå, Sweden

<sup>3</sup>Geography, School of Human and Life  
Sciences, Canterbury Christ Church  
University, Canterbury, UK

## Correspondence

Richard J. Mason, Department of Ecology  
and Environmental Sciences,  
Umeå University, Umeå, Sweden.  
Email: richard.mason@umu.se

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## Abstract

Invertebrates are important sediment engineers, making up for their small body size with abundance and behavioral diversity. However, despite the recognized importance of invertebrates as sediment engineers in terrestrial and marine environments, zoogeomorphology in rivers has primarily considered larger taxa, such as fish and beaver. This article reviews the zoogeomorphic effects of invertebrates in freshwater habitats, with a focus on rivers. To better synthesize current zoogeomorphic research and to help guide future studies we build a conceptual model considering biotic (behavior, abundance, body size, life history, and species invasions) and abiotic (geophysical energy and sediment grain size) controls on the direction and magnitude of zoogeomorphology. We also incorporate invertebrate engineers into conceptual sediment entrainment models, to understand their geomorphic role in the context of hydraulic power and sediment size. We structure our review around invertebrate behavior as a key control on whether invertebrates have a sediment destabilizing or stabilizing impact. Invertebrate zoogeomorphic behavior are diverse; the majority of research concerns *bioturbation*, a result of locomotion, foraging, and burrowing behaviors by many taxa. Similarly, burrowing into bedrock by a caddisfly and non-biting midge larvae promotes *bioerosion*. Attachment to the substrate, (e.g., silk nets by caddisfly larvae or byssal threads by some mussels) can stabilize sediment, providing *bioprotection*. *Bioconstructions* (e.g., caddisfly cases and mussel shells) may have either stabilizing or destabilizing effects depending on their density and abiotic context. Interactions between lotic invertebrates and fluvial processes are complex and understudied, requiring further research across a greater range of taxa, behaviors, and spatiotemporal scales.

This article is categorized under:

Water and Life > Nature of Freshwater Ecosystems

Water and Life > Conservation, Management, and Awareness

## KEYWORDS

biogeomorphology, fine sediment, invertebrate behavior, sediment transport, zoogeomorphology

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## 1 | INTRODUCTION

Recognition of the importance of biology in landform development represents a paradigm shift within geomorphological research (Corenblit et al., 2007; Viles, 1988). The discipline of *biogeomorphology* considers how living organisms affect sediment processes (Naylor et al., 2002; Viles, 1988), while *zoogeomorphology* specifically considers the sediment engineering role of animals (Butler, 1992, 1995). Biogeomorphic and zoogeomorphic research demonstrates that organisms of all sizes, from grizzly bears (Butler, 1992) to microbes (Le Hir et al., 2007; Viles, 2012), can have large-scale effects on sediment transport processes.

Eighty percent of known animal species on earth are invertebrates (Darwall et al., 2012). Invertebrates provide an immeasurable range of ecosystem services (Prather et al., 2013) and have important zoogeomorphic effects (Albertson & Allen, 2015; Bétard, 2020). Charles Darwin's (1881) research on the role of worms in terrestrial landform development is often cited as the first reference to an animal zoogeomorphic agent (Coombes, 2016; Meysman et al., 2006; Rice et al., 2019). Darwin wrote "Worms have played a more important part in the history of the world than most persons would at first suppose" (Darwin, 1881, p. 305). However, invertebrate zoogeomorphic activities were recognized much earlier. In 1713, in Piedade no Maranhao, Brazil, a colony of termites was excommunicated from the Catholic Church for burrowing under a monastery wall, destabilizing it (Evans, 1906). Subsequent research has shown that invertebrates, particularly worms, ants, and termites, are pervasive sediment engineers in terrestrial landscapes (Dangerfield et al., 1998; Meysman et al., 2006; Whitford & Eldridge, 2013; Wilkinson et al., 2009). In marine and estuarine environments, invertebrates are important modifiers of sediment structure and porosity (Mermillod-Blondin & Rosenberg, 2006; Murray et al., 2002; Shull, 2008), and a "burrowing revolution" approximately 542 million years ago is believed to have altered geochemical functioning of the ocean, contributing towards the Cambrian Explosion (Babcock, 2005; Thayer, 1979).

In rivers, however, biogeomorphic research has principally considered vegetation and larger vertebrate animals (Albertson & Allen, 2015; Gurnell et al., 2019; Polvi & Sarneel, 2018; Rice et al., 2012; Statzner, 2012). Beaver dams act as traps for water and sediment (Brazier et al., 2021; Gurnell, 1998; Naimen et al., 1988; Puttock et al., 2018; Ruedemann & Schoonmaker, 1938). Spawning salmon and trout construct redds (nests), disturbing the protective coarse sediment surfaces (armor) of river beds and increasing sediment transport (DeVries, 2012; Fremier et al., 2018; Hassan et al., 2011). Similarly, benthivorous fish disturb sediment when feeding from the river bed substrate (Booth et al., 2020; Pledger et al., 2017; Rice et al., 2019).

The focus of fluvial zoogeomorphic research on larger taxa may be attributable to lesser awareness of small animals (Darwall et al., 2012; Strayer, 2006). However, while small, invertebrates are ubiquitous across freshwater systems (CEH, 2021), including those that may not support higher orders of taxa such as fish. Invertebrates often exist at very high population density and biomass. Invertebrate density commonly exceeds  $1000\text{ m}^{-2}$  (Cardinale et al., 2004; Strayer, 2006) and sometimes exceeds  $10^6\text{ m}^{-2}$  (Palmer, 1990; Strayer, 1985). Invertebrates underpin the ecological functioning of river environments and support higher order biodiversity (Covich et al., 1999; Wallace & Webster, 1996). While individual impacts may be small, invertebrate populations can have zoogeomorphic effects in rivers comparable to those of much larger taxa (Albertson & Allen, 2015).

Freshwater invertebrates are extraordinarily diverse, comprising 86% of freshwater animal species (Balian et al., 2008). Freshwater invertebrates are also functionally diverse, exhibiting behaviors that facilitate large zoogeomorphic effects. For example, many invertebrate taxa erode sediment by burrowing (Faller et al., 2016; Rice et al., 2016; Sanders et al., 2021), while others consolidate sediment by building stabilizing structures (Albertson et al., 2019; Johnson et al., 2009). Consequently, invertebrates can have a diverse array of zoogeomorphic effects, mediated in part by their behavior.

This article reviews the zoogeomorphic effects of freshwater invertebrates, with a focus on rivers, and refines existing conceptual models of biotic and abiotic controls on zoogeomorphology. Specifically we frame our review around the links between invertebrate behavior and their zoogeomorphic effects. We consider the interaction between invertebrate zoogeomorphology and geophysical power in rivers, integrating existing conceptual models of biological controls on zoogeomorphology (e.g., Moore, 2006) with physical models of sediment entrainment (e.g., Hjulström, 1935; Shields, 1936). Thus, we provide a summary of the state of scientific understanding of lotic invertebrate zoogeomorphology, and a conceptual framework to guide future research and enhance understanding of the mechanisms by which invertebrates affect sediment dynamics in rivers.

## 2 | A REVIEW OF LOTIC INVERTEBRATE ZOOGEOMORPHOLOGY

The diversity of riverine invertebrates results in a wide range of effects on sediment processes in rivers (Box 1), including most of those effects documented for both plants and animals (Corenblit et al., 2011; Naylor et al., 2002; Viles, 2019). Freshwater invertebrates also affect sediment dynamics via biogeomorphic effects not recognized for other taxa, such as via biofiltration (Box 1). The chemical erosion of solid substrates by biological organisms is termed bioweathering. While ants are known to cause terrestrial bioweathering (e.g., Dorn, 2014), we are not aware of any instances of invertebrate bioweathering in rivers.

### Box 1 Zoogeomorphic effects of freshwater invertebrate taxa

#### (i) Bioerosion

Degradation of hard surfaces by organisms (e.g., caddisfly larvae burrowing into bedrock).

#### (ii) Bioturbation

Biotic reworking of loose sediment (e.g., resuspension of sediment by foraging shrimp).

#### (iii) Biofiltration

Removal of fine particulate matter from the water column. Exhibited by filter feeders such as molluscs and caddisfly larvae silk filter nets.

#### (iv) Bioprotection

The accumulation or stabilization of sediment (e.g., sediment stabilization by caddisfly larvae silk nets).

#### (v) Bioconstruction

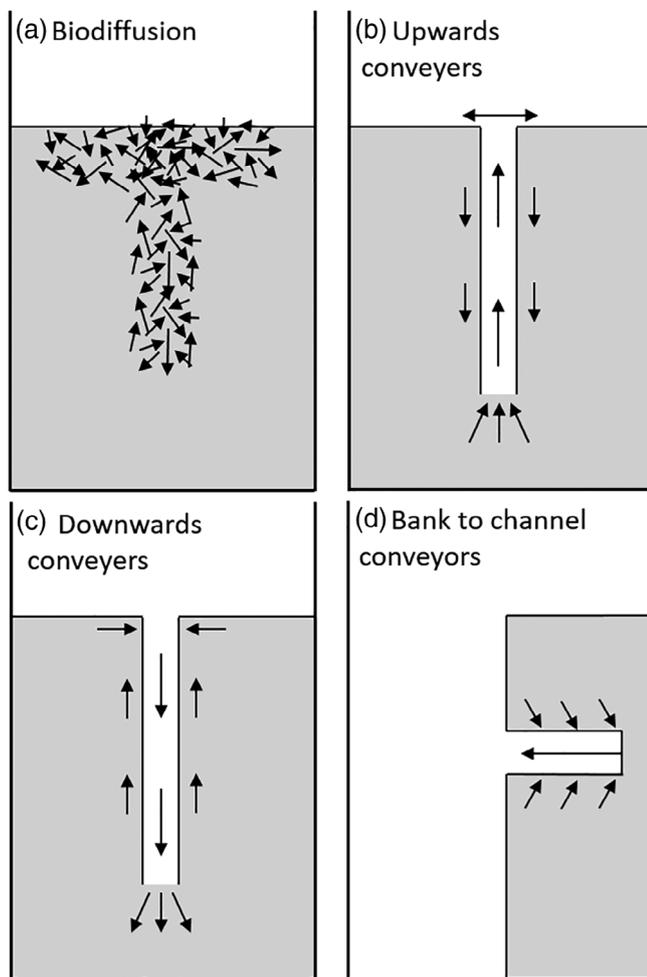
Structures built by organisms. Bioconstructions may be allogenic, using material external to the organism (e.g., caddisfly larvae cases) or autogenic, using self-generated tissue (e.g., mollusc shells).

We structure our review around the organism behaviors documented to have zoogeomorphic effects. These behaviors are; (1) behaviors relating to organism movement, specifically locomotion (e.g., stonefly larvae; Statzner et al., 1996), and attachment (e.g., via silk threads to prevent drift; Cardinale et al., 2004; Kiel, 2001), (2) feeding behaviors, specifically foraging (e.g., mayfly larvae; Soluk & Craig, 1990) and filtering of fine sediment from the water column by filter feeding organisms (e.g., mussels; Rosa et al., 2018), (3) burrowing into both the river bed (e.g., midge larvae; Savrda, 2019) and river banks (e.g., signal crayfish; Sanders et al., 2021), and (4) the creation of structures (e.g., caddisfly larvae cases; Mason et al., 2019). In addition to lotic invertebrate zoogeomorphic literature, we reinterpret research from disciplines of ecosystem engineering (Jones et al., 1994) and ichnotaxonomy (e.g., Savrda, 2019), and functionally similar invertebrates in lentic and marine environments (e.g., Charbonneau & Hare, 1998; Meysman et al., 2006). Due to the available literature, this review is necessarily restricted to the larger invertebrate groups, easily visible to the naked eye (macroinvertebrates; specifically insects, crustaceans, and molluscs).

### 2.1 | Bioturbation and bioerosion

Bioturbation and bioerosion (Box 1i and ii) redistribute sediment, changing both the physical structure of substrates and the chemical and biological processes occurring within (Gautreau et al., 2020; Mermillod-Blondin, 2011). Bioerosion (Box 1i) is exhibited by taxa which burrow into rock or consolidated bed and bank sediment (Sanders et al., 2021; Savrda, 2019). Bioturbation (Box 1ii) is the most researched biogeomorphic effect in rivers (Albertson & Allen, 2015; Statzner, 2012) and is a product of several mechanisms (Figure 1).

Aquatic invertebrates cause bioturbation directly by moving about on the river bed surface (during locomotion and foraging), and indirectly, by modifying near surface hydraulics. For example, crayfish disturb sediment directly when walking (Pond, 1975) and indirectly by hydraulic disturbance through tail thrusting during escape (Webb, 1979). Locomotion within unconsolidated sediments can suspend fine grained sediment, and larger invertebrates can also redistribute coarser gravel particles (Johnson et al., 2010).



**FIGURE 1** Mechanisms of bioturbation (adapted from Kristensen et al., 2012 with D added to suit lotic environments). (a) Biodiffusion—movement of particles short distances in effectively random directions, vertically or horizontally. (b) Upwards conveyers—behaviors resulting in a net movement of sediment upwards. (c) Downwards conveyers, (d) bank to channel conveyers—taxa which burrow into river banks and increase bank erosion and fine sediment input into the channel

Bioturbation typically involves moving particles short vertical or horizontal distances causing mixing (biodiffusion; Figure 1a; François et al., 1997). Due to the heterogeneous nature of river hydraulics, the transport of sediment relatively short distances (particularly vertically) can result in large differences in exposure to entraining forces (Johnson et al., 2011; Rice et al., 2019). Some taxa may also preferentially move particles upwards or downwards through the river bed (Figure 1b,c). In rivers, channel banks are an important source of sediment, the supply of which can be augmented by bank burrowing organisms (Figure 1d).

### 2.1.1 | Locomotion and foraging

Most macroinvertebrate taxa are mobile and therefore have the potential to disturb bed sediments during locomotion, usually resulting in biodiffusion (Figure 1a). Bioturbation activities may increase when activity levels increase, such as when foraging for food. Crayfish have been a focus for lotic invertebrate zoogeomorphic research. Their locomotion and foraging behaviors, relatively large size and successful invasion into new territories (Kouba et al., 2014) allow them to have substantial effects on sediment transport (Harvey et al., 2014; Rice et al., 2016). Several species of crayfish are documented to bioturbate sediment, including the rusty crayfish (*Faxonius rusticus*; Albertson & Daniels, 2016a; Statzner et al., 2000; Statzner & Peltret, 2006), red swamp crayfish (*Procambarus clarkii*; Arce & Diéguez-Urbeondo, 2015), and the signal crayfish (*Pacifastacus leniusculus*; Harvey et al., 2014; Johnson et al., 2010; Rice et al., 2014). Crayfish locomotion in gravel substrates results in pits and mounds (Albertson & Daniels, 2016a; Johnson et al., 2010), affects near bed hydraulics (Han et al., 2019), and leads to the suspension of fine sediment (Harvey et al., 2014).

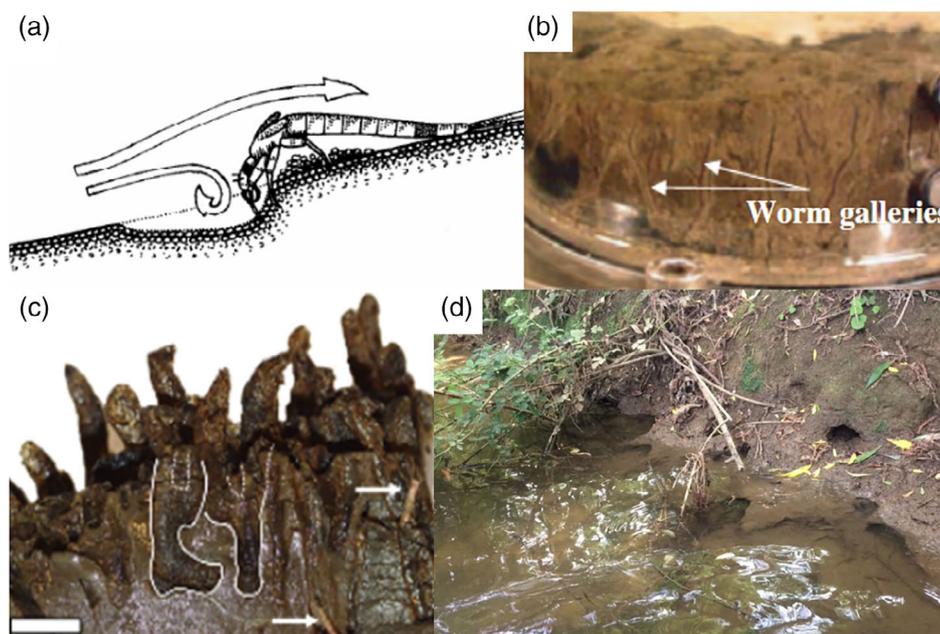
Pringle et al. (1999) identify shrimp as important ecosystem engineering agents, likening them to “megaomnivores,” due to high population densities (up to  $25 \text{ m}^{-2}$ ; Pringle & Blake, 1994), seasonally persistent presence in rivers and high mobility and feeding rates. Atyidae (shrimp) reduce sedimentation of both organic and inorganic fine particulates in

depositional environments; 100% of sediment deposited on experimental ceramic tiles was removed in the 30 min following shrimp access (Pringle et al., 1993), and shrimp reduced benthic fine sediment concentrations by 35% in stream-bed enclosure experiments (Pringle & Hamazaki, 1998).

Insects can also cause bioturbation via locomotion and foraging. Predatory stonefly larvae can transport substantial quantities of sand out of gravel interstices while foraging for prey (up to  $200\text{--}400\text{ kg m}^{-2}\text{ a}^{-1}$  for *Dinocras cephalotes*; Statzner et al., 1996), with reduced prey availability increasing foraging activity, and therefore erosion (Statzner et al., 1996; Zanetell & Peckarsky, 1996). *Pseudiron centralis* (mayfly) larvae create hydraulic structures which erode sand furrows to hunt for buried Chironomidae larvae (non-biting midge; Soluk & Craig, 1990; Figure 2a). Furthermore, bioturbation by the caddisfly *Pycnopsyche gentilis* excavates buried organic matter, beneficial for other invertebrates (Creed et al., 2010). In a pool of a small, low-order stream, bioturbation by the resident invertebrate communities resulted in 85% of the surface reworked after 4 days (De Nadaï-Monoury et al., 2013). A number of insects were responsible, and included cranefly (Tipulidae), dragonfly (Odonata), and two caddisfly taxa; Odontoceridae and Sericostomatidae (De Nadaï-Monoury et al., 2013).

The distribution of interstitial benthic sediments is important to consider because they influence subsurface hydraulic connectivity and the flow of oxygen and nutrients (Gautreau et al., 2020; Mermillod-Blondin & Rosenberg, 2006), affecting both the ecology and the physical structure of benthic substrates (Nogaro et al., 2006). In modifying interstitial sediments, invertebrates may affect river bed colmation (the clogging and infilling of interstitial spaces by fine sediment), a widespread problem in rivers (Waters, 1995; Wharton et al., 2017). Bioturbation may promote decolmation (Mermillod-Blondin, 2011; Nogaro et al., 2006; Wharton et al., 2017) but may also increase infiltration of fine sediment into interstices (Mathers et al., 2019). This can have consequences both for stream ecosystem function and sediment dynamics.

The timing of fine sediment transport is also important ecologically because fine sediment is associated with deoxygenation (Ryan, 1991) and the transport of pathogens (Bai & Lung, 2005; Hassard et al., 2016), the effects of which may be more dilute during higher flow events. Therefore, fine sediment released by bioturbation in base flow by zoogeomorphic mechanisms (e.g., by signal crayfish; Rice et al., 2016) may be more damaging than fine sediment entrained during winter floods. Fine sediment content is also important to the transport of coarser sediment, both by



**FIGURE 2** Examples of lotic invertebrate bioturbation and bioerosion. (a) Bioturbation by mayfly larvae (*Pseudiron centralis*) which uses body positioning to create hydraulic structures eroding sand furrows to excavate prey (reproduced from Soluk & Craig, 1990). (b) Galleries of Tubificidae worms (*Tubifex* sp. and *Limnodrilus* sp.) increase hydraulic connectivity of the subsurface and convey fine sediment to the surface (reproduced from Nogaro et al., 2006). (c) Bioerosion by caddisfly larvae, which build Y-shaped burrows which extend 40 mm into mudstone (white outline) accompanied by smaller U-shaped Chironomidae burrows (white arrows; scale bar = 1 cm; reproduced from Savrda, 2019). (d) Burrows of signal crayfish (*Pacifastacus leniusculus*) in Gaddesby Brook, UK

burying and consolidating coarser grains and by reducing bed roughness allowing coarser grains to travel further over the river bed (overpassing; Carling, 1990; Isla, 1993), depending on fine sediment content (Grams & Wilcock, 2007; Venditti et al., 2010; Wilcock et al., 2001). Statzner (2012) estimated that stonefly (*D. cephalotes*) bioturbation which removed fine sediment from interstices between coarse grains could increase cobble critical entrainment thresholds by 50% (following Wilcock & Kenworthy, 2002).

### 2.1.2 | Vertical burrowing

Considerable research has considered vertical burrows (Kristensen et al., 2012; Figure 1b,c), such as those constructed by isopods and crabs in estuarine environments (e.g., Escapa et al., 2007; Smith & Green, 2015; Talley et al., 2001; Wilson et al., 2012). For example, burrows of the crab *Neohelice granulata* can exist in densities of 172 burrows  $\text{m}^{-2}$  (Angeletti et al., 2018) and remove up to  $147.5 \text{ g d}^{-1}$  of sediment per burrow (Iribarne et al., 1997). Vertical crab burrows have thus been associated with accelerated marsh creek formation through the exclusion of stabilizing vegetation, and directly by destabilizing sediment (Escapa et al., 2007), with the associated creek development hypothesized to mitigate the effects of sea level rise on saltwater incursion (Vu et al., 2017).

As well as supplying sediment to the water column, vertical burrowing redistributes sediment within the subsurface upwards and downwards through both biotic and gravitational energy (Figure 1b,c). Similar to terrestrial worm activity documented by Darwin (1881), in freshwater environments, Oligochaeta (worms) feeding on material up to 20 cm below the sediment surface transport this to the surface as fecal pellets (Ciutat et al., 2006; Dafoe et al., 2011; Figure 1b and 2b). Networks of burrows constructed by Tubificidae (Oligochaeta) increase interstitial flow within fine-grained benthic sediments (Nogaro et al., 2006), modify lake sediment structure, and increase suspended sediment (Zhang et al., 2014). While Tubificidae create accumulations of fine sediment at the river-bed surface, Asellidae (water hoglouse) and Chironomidae accumulate sediment approximately 5 cm below the surface (Mermillod-Blondin et al., 2002). Chironomidae build U-shaped tubes within the top layer of sediment (Nogaro et al., 2006). In a flume experiment considering the spatial distribution of *Lumbriculus variegatus*, an upward conveying worm, Lakhanpal (2018) found galleries on average  $1.5\text{--}2 \text{ mm}^3$  in volume, concentrated in the top 2 cm of sediment, where they are most likely to affect sediment dynamics on the surface.

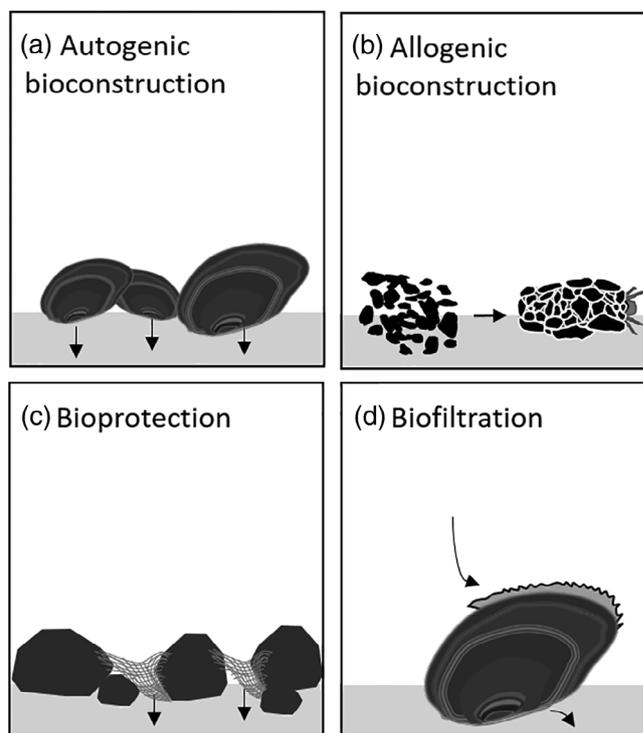
Mayfly in lakes are also documented to have bioturbation effects, by burrowing or dwelling in interstices (Bae & McCafferty, 1995; Charbonneau & Hare, 1998; Edmunds & McCafferty, 1996). Individual *Hexagenia limbata* (mayfly) larvae can move an average of  $4 \text{ cm}^3$  sediment per day (Charbonneau & Hare, 1998). Mayfly burrowing is not limited to loose sediment, and also causes bedrock bioerosion (Box 1; Davidson et al., 2018). Uchman et al. (2017) documented U-shaped burrows of mayfly in consolidated sediment from the rivers Drwęca (Poland) and Ohře (Czechia). Similarly, Savrda (2019) found Chironomidae burrows (in claystone) and caddisfly burrows up to 40 mm deep in claystone and sandstone in the Conecuh River, USA (Figure 2c). Caddisfly burrows were extended above the riverbed surface by chimneys of fine sediment (Savrda, 2019).

Biotic modification to interstitial flow and sediment concentrations may have important implications for nutrient and oxygen delivery and waste removal (Greig et al., 2005; Sarriquet et al., 2007). While the primary geomorphic effects of vertical burrows (direct sediment movement) have been studied, secondary effects (e.g., accelerated erosion) have not been quantified.

### 2.1.3 | Horizontal burrowing

Rivers differ from marine and estuarine environments by providing a greater availability of vertical surfaces, in the form of river banks (Figures 1d and 3d). Understanding the process of riverbank burrowing is important, because as well as directly supplying sediment (Harvey et al., 2014), riverbank burrowing can also accelerate bank erosion and collapse, inputting more sediment into the river channel (Harvey et al., 2019; Sanders et al., 2021). Harvey et al. (2019) suggest that burrowing may augment physical processes through three major mechanisms. First, burrows may modify the spatial distribution of pore water pressure in the river bank and reduce the length of failure planes. Second, changes to local hydraulics can modify near bank flow structures. Last, burrowing may remove stabilizing vegetation, and alter biofilm and fungal networks. These hypotheses have been supported by physical modeling (Saghaee et al., 2017; Viero et al., 2013) and numerical modeling (Borgatti et al., 2017; Camici et al., 2014; Orlandini et al., 2015).

**FIGURE 3** Mechanisms for sediment stabilization by aquatic animals. (a) Bioconstruction using self-generated tissue, for example mussel shells or caddisfly nets. (b) Bioconstruction using other materials, for example the construction of cases by many caddisfly species. (c) Bioconstructions may stabilize bed sediments via bioprotection (e.g., caddisfly filter feeding nets tie gravel particles together). (d) Filtration of fine sediment from the water column by feeding organisms



Semi-quantitative field observations in the UK (Faller et al., 2016) and the Iberian Peninsula (Arce & Diéguez-Uribeondo, 2015; Barbaresi et al., 2004) have suggested that the presence of animal burrowing can increase the probability of riverbank collapse. Faller et al. (2016) estimated that signal crayfish add approximately  $3 \text{ t km}^{-1}$  of sediment in burrowed sections of the Thames catchment, UK, but burrowing was patchy and occurred at only 10% of banks surveyed. Sanders et al. (2021) provide the first long term (22-month) empirical field evidence of a relationship between burrows and accelerated bank retreat and collapse. By destabilizing river banks, signal crayfish may supply more than 49 times as much sediment to river systems than burrowing alone, with accelerated retreat supplying  $25.4 \text{ t km a}^{-1}$  of additional sediment to a UK lowland river, contributing 12% of total sediment supply from riverbanks at the reach scale (Sanders et al., 2021). However, the mechanisms underpinning these changes outlined in Harvey et al. (2019) are not yet understood, and are thus an important avenue of future research.

## 2.2 | Bioprotection and bioconstruction

There are fewer examples of sediment stabilization than destabilization in lotic zoogeomorphology, and most stabilizing taxa are invertebrates (Albertson & Allen, 2015). The diverse behaviors of aquatic invertebrates are key to their sediment stabilization. Invertebrates which produce biogenic secretions such as mussel shells, silk threads, or byssal threads have particularly important zoogeomorphic effects. Several aquatic insect orders (Trichoptera, Diptera, and Lepidoptera) and some arthropods secrete silk. Silk is a tough, fibrous, protein used by organisms in tube construction, feeding nets, and to attach themselves and their structures to the substrate (Wotton, 2011). The majority of research on the importance of silk to zoogeomorphology in rivers has considered the biostabilizing effects of caddisfly (Trichoptera). Similar to silk, byssus is a filamentous thread secreted by many bivalve species for attachment to surfaces, including river gravels (Peyer et al., 2009). These secretions can act to anchor sediment, providing bioprotection, or may affect sediment mobility via bioconstruction (Box 1).

The effects of bioconstruction (Box 1iv) and bioprotection (Box 1v) are difficult to separate. Bioconstructions which are fixed in place (e.g., by byssal threads or silk) usually stabilize sediment (Jones et al., 1994; Viles, 2019). Invertebrate bioconstructions such as the filter feeding nets of caddisfly larvae also provide bioprotection, since they act to tie sediment together on the river bed and reduce entrainment (Johnson et al., 2009; Statzner, 2012). However, bioconstruction may also destabilize sediment by increasing the mobility of incorporated sediment or moving sediment to a more exposed location (Fei et al., 2014).

## 2.2.1 | Construction

Autogenic bioconstructions are built from secretions generated by the organism (Jones et al., 1994; Figure 3a). In rivers, autogenic bioconstructions include the shells of molluscs (Gastropods and Bivalves). However, while marine research has demonstrated that mussel beds can stabilize sediment (Widdows et al., 2009), there has been little freshwater research (Gutiérrez et al., 2003). Zimmerman and de Szalay (2007) studied the effects of two unionid mussels (mucket mussel, *Actinonaias ligamentina* and kidney shell mussel, *Ptychobranhus fasciolaris*) on sediment stability in an experimental river channel. The zoogeomorphic effects were complex and related to organism behavior. Unionid mussels initially increased bioturbation via locomotion and burrowing but when mussels were more sessile (after 4 weeks) they increased the shear strength of bed sediment by 24% over controls (Zimmerman & de Szalay, 2007).

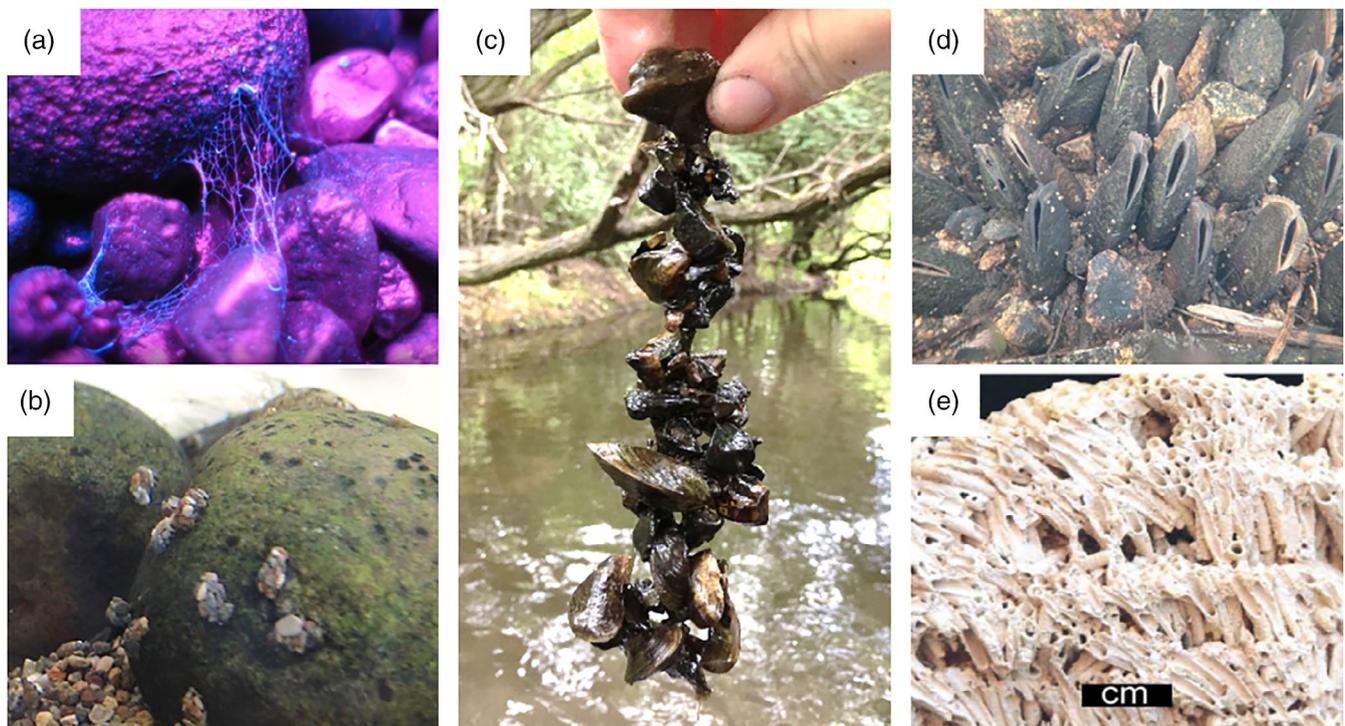
Large mussels may have a stabilizing effect due to their weight and size, which if greater than the underlying bed sediment can provide bioprotection (Figure 3c). Furthermore Zimmerman and de Szalay (2007) found that unionid mussels compressed the bed sediment by 31% which may also increase resistance to erosion. Mussels also affect the hydraulics near the bed surface. Sansom et al. (2020) found that at densities of 25 m<sup>-2</sup> or more, shear stress acting on mussels reduced by 64% and shear stresses at the bed were much reduced. Research with functionally similar taxa in marine environments has found that a 25%–50% bed coverage the marine edible mussel (*Mytilus edulis*) creates turbulent hydraulic structures which may increase local shear stresses and thus promote sediment transport (Widdows et al., 2002). In contrast, high densities of mussels may reduce near bed flow velocities (Nowell & Church, 1979; Nowell & Jumars, 1984; Widdows & Brinsley, 2002) and thus sediment transport.

Caddisfly (Trichoptera) are an order of aquatic insects known for their creation of structures, including silk capture nets and cases (Wiggins, 2004). While caddisfly nets are autogenic bioconstructions, we consider them in the attachment section as the primary mechanism by which they affect sediment stability is thought to be by attaching particles together and binding them to the river bed (bioprotection; Johnson et al., 2009; Statzner et al., 1999). Caddisfly cases can be classed as allogenic bioconstructions since they are typically built from mineral and organic sediment fastened together with silk (Wiggins, 2004; Figure 3b). Cases are built by most caddisfly species at some point in their lifecycle as most free-living and net building taxa typically also build cases for pupation (Statzner et al., 2005; Wiggins, 2004). Caddisfly incorporate a wide range of sediment grain sizes, depending on species (0.063–4 mm for mobile cases), while taxa that construct fixed pupal cases can use larger particles (~ 11 mm; Mason et al., 2019). In a lowland gravel-bed UK stream, 94% of caddisfly species used mineral sediments for case building (mean abundance = 2250 larvae m<sup>-2</sup>) and resulted in a mean mass of incorporated sediment of 38 g m<sup>-2</sup> (Mason et al., 2019).

The effect of caddisfly case bioconstructions on the stability of sediment is unknown. When cases are fixed in place they probably increase sediment stability (Statzner, 2012) and caddisfly pupal cases were found to fix up to 40% of specific grain size fractions in the bed surface of the Furan River, France (Statzner et al., 2005), although this proportion of sediment use is probably exceptional (Mason et al., 2019). In contrast, many case-building caddisfly are very mobile and travel many meters over the river bed per day transporting their case and incorporated sediment with them (Erman, 1986; Jackson et al., 1999; Lancaster et al., 2006), causing bioturbation. Consequently, the direction of zoogeomorphic effect of case-building by caddisfly may vary based on species, life stage (many cases are fixed to larger particles at pupation), and the abiotic environment.

Sediment stabilization by silk from other insect taxa is less well studied. Chironomidae larvae also use fine sediment (organic and inorganic materials) in the construction of tubes which function for feeding, respiration, and to prevent predation (Brennan & McLachlan, 1979; Hershey, 1987). Edwards (1962) found that Chironomidae tubes act to reduce suspension of fine sediment from mud substrates; Statzner (2012) reports this may decrease sediment mobilization by 90%. Furthermore, Chironomidae tubes may reduce the exposure of bed sediments by altering hydraulic flows and reducing bed shear stresses (Ólafsson & Paterson, 2004).

Invertebrate biostructures, including cases of caddisfly (Figure 4e), can provide a stable spot for calcium carbonate to deposit (Roche et al., 2019), resulting in bioherms (accretionary mounds consisting of fossilized remains surrounded by different geology; Cummings, 1932). In Western China, He et al. (2015) recorded caddisfly bioherms 3–5 m high stretching 400–500 m laterally. Similarly, bioherms predominantly composed of layers of caddisfly cases and calcium deposits line the shores of Lake Gosiute, Wyoming, USA (Leggitt & Cushman, 2001). These bioherms are extensive; 70 km in length, 9 m in height, and 40 m in diameter (Leggitt & Cushman, 2001).



**FIGURE 4** Examples of bioprotection and bioconstruction by invertebrate animals in rivers. (a) Nets of Hydropsychidae caddisfly nets fluorescing under UV light (image: Matthew Johnson). (b) Case-building caddisfly larvae (Glossosomatidae) move sand around the sediment–water interface. (c) Quagga mussels attach to bed sediment and other mussels using byssal threads, River Wraysbury, UK. (d) Populations of freshwater mussels may stabilize sediment and filter suspended sediment from the water column (image: freshwater pearl mussels with Glossosomatidae caddisfly living on them). (e) Layers of caddisfly cases form calcium carbonate bioherms. Each caddisfly case is orientated vertically: reproduced from Leggitt and Cushman (2001)

### 2.2.2 | Attachment

Bioconstructions are likely to have greater bed stabilization effects if attached to the bed surface by silk or byssal threads. Zebra (*Dreissena polymorpha*) and quagga mussel (*D. rostriformis bugensis*) are invasive in Europe and North America (Mills et al., 2019; Strayer et al., 1999) and use byssal threads to anchor themselves to river bed substrate. Byssal threads may be an important stabilizing agent of gravel beds by binding gravel particles together and increasing their effective size (Figure 4c). Byssal threads are resistant to physical forces; after 3 months of attachment, forces of 1.6 and 1.7 N were required to break byssal threads of zebra and quagga mussels, respectively (Dormon et al., 1997). Furthermore, byssal threads can persevere in the environment long after the mussels have died (Burlakova et al., 2000). However, the zoogeomorphic implications of byssal thread anchoring by these species are unknown. Both species can expand ranges at very high rates (mean 120 km a<sup>-1</sup> NW Europe; Matthews et al., 2014) reaching densities exceeding 1000 individuals m<sup>-2</sup> (Nalepa et al., 2009; Strayer et al., 1999) and therefore further research into their effects on sediment stability is important.

Many caddisfly species construct capture nets and fixed retreats from silk, strung between sediment particles in running water (Figure 4a). The nets allow the caddisfly to catch food drifting downstream and, not being reliant on food resources from their immediate surroundings, can reach very high densities >1000 m<sup>-2</sup> (Cardinale et al., 2004; Oswood, 1979; Statzner et al., 2005). Caddisfly silk is very stretchy and can more than double in length before breaking (Brown et al., 2004; Tszedel et al., 2009). Consequently caddisfly structures can be long lasting (Albertson & Daniels, 2016b); in situ (Tumolo et al., 2019) and ex situ (Maguire et al., 2020) experiments have measured silk produced by Hydropsychidae caddisfly larvae to persist in the environment for up to 30 and 60 days post abandonment, respectively. This silk has important geomorphic effects; the construction of nets and retreats from silk by caddisfly larvae ties particles together, increasing their effective size and binding them to the river bed (Albertson et al., 2019; Albertson, Sklar, et al., 2014). For example, Johnson et al. (2009) found that a polyculture of Hydropsychidae species (71% of larvae were

*Hydropsyche contubernalis*) colonized field-deployed trays of gravels at natural densities (1240–4737 larvae  $m^{-2}$ ), resulting in a 23%–35% increase in the shear stress required to entrain gravels. Even greater bed stabilization effects have been found in controlled flume experiments for *Ceratopsyche oslari* (mean critical shears stress increase = 57%, mean density = 2460 larvae  $m^{-2}$ ) and *Artopsyche californica* (109%, 1530 larvae  $m^{-2}$ ; Albertson, Cardinale, & Sklar, 2014). *Stenopsyche marmorata* retreats fixed with silk between large cobbles can increase the mean force required to move a cobble (50–60 mm diameter) 2–3 fold for a single retreat (Nunokawa et al., 2008).

The differences in documented sediment stabilization by net building caddisfly between studies may be attributed to differences in experiment design and methods used to measure incipient motion and critical shear stress (Perret et al., 2015; Vanoni, 2006) as well as differences between the abundances and behavior of species investigated. Larger caddisfly taxa, with stronger silk, result in greater sediment stabilization. *A. californica* capture nets are 20% stronger than nets of *C. oslari* (Albertson, Sklar, et al., 2014) and have nearly double the stabilizing effect (Albertson, Cardinale, et al., 2014). Caddisfly nets have significant stabilizing effects on gravel 4–65 mm in diameter (Albertson, Sklar, et al., 2014; Nunokawa et al., 2008), but at larger particle sizes, the greater mass of large grains may dwarf the stabilizing effects of caddisfly (Johnson et al., 2009). When multiple species of net-building caddisfly taxa are present they may change their behavior (Albertson et al., 2019). In polyculture, *A. californica* and *C. oslari* constructed nets at different heights in gravel interstices, further increasing bed stability (mean critical shears stress increase = 150%, 1933 larvae  $m^{-2}$ ; Albertson, Cardinale, et al., 2014).

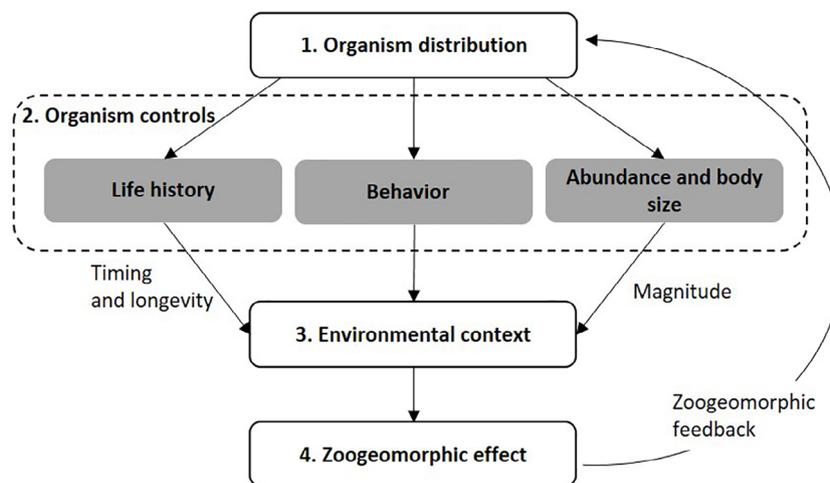
Furthermore, caddisfly nets also reduce near bed horizontal flow velocities (Maguire et al., 2020) and within bed vertical hydraulic conductivity (MacDonald et al., 2020) by providing flow resistance. Juras et al. (2018) used a computer model simulating caddisfly nets as solid barriers within pore spaces between gravel particles. At a density of 735 nets  $m^{-2}$ , average shear stress on the bed was reduced by 11.6% (Juras et al., 2018). However, this provides an upper estimate for the flow velocity reduction of caddisfly, because nets typically have high porosity (Edler & Georgian, 2004; Juras et al., 2018). A six times enlarged scale model of a *Ceratopsyche sparna* net in a flume reduced streamwise velocity in the vicinity behind the net by 45% at  $0.71 m s^{-1}$ , but this effect was reduced at higher flow velocity (Edler & Georgian, 2004).

Biostabilization also has ecological impacts (Silknetter et al., 2020). For example, biostabilization may create stable patches which act as refugia for the engineering organism and other species during high flows (Cardinale et al., 2004), and may also increase habitat complexity for other organisms. Mussel shells provide a stable and heterogeneous habitat for diverse communities (Mills et al., 2019; Spooner & Vaughn, 2006; Sylvester et al., 2007) and the presence of caddisfly and silk nets in a stream in Pennsylvania, USA, increased total invertebrate density by 25% (Tumolo et al., 2019).

## 2.3 | Biofiltration

Biofiltration considers the removal of fine material from the water column (Box 1iii), which predominantly occurs as a feeding mechanism. The ecological effects of biogeochemical cycling by suspension feeding bivalves have been well studied (Vaughn & Hakenkamp, 2001; Vaughn & Hoellein, 2018). The removal of suspended fine particulate matter can significantly reduce turbidity, promote macrophyte and algae growth (Ozersky et al., 2013), and change ecological community dynamics (De Stasio et al., 2014; Vanderploeg et al., 2001). Filter feeding may also have considerable geomorphic effects, such as reduced downstream fine sediment transport. While filter feeding organisms feed on organic material in the water column (e.g., algae, microbes, zooplankton, and detritus), filtering material also contains inorganic particles (Rosa et al., 2018; Tuttle-Raycraft & Ackerman, 2018). Research in the marine environment shows that filtering may also have geomorphic effects for bed sediments, with the biological deposition of filtered material increasing sedimentation rates by up to 40 times (Widdows et al., 1998; Figure 3d).

The upscaling of mesocosm experiments has demonstrated noteworthy clearance rates of small coastal and estuarine environments, such as the complete filtration of North Inlet, South Carolina, USA, in less than 1 day (Dame & Prins, 1998). However, lotic systems are more hydraulically dynamic than estuarine systems, and so the biological capacity for filtration may need to be greater in the riverine environment to achieve the same filtration effects; filtering capacity would have to allow for both sediment production rates and river discharge. Upscaling calculations have suggested that unionid filtration has the capacity to exceed discharge by an order of magnitude during low flow conditions in an Oklahoma river, USA (Vaughn, 2010), but the associated sediment dynamics and temporal importance of this are unknown.



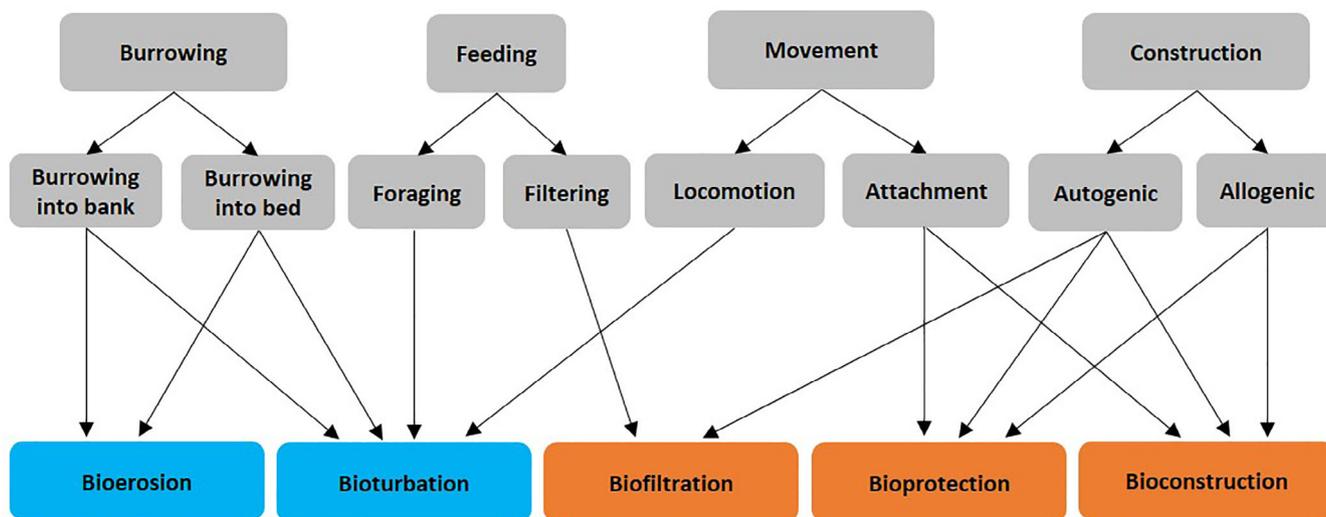
**FIGURE 5** Conceptual model for the zoogeomorphic effects of animals highlighting the importance of organism traits (gray boxes). Adapted from Moore (2006) who considered how behavior, body size and abundance are mediated by abiotic context to influence zoogeomorphic affects. (1) The spatial distribution of zoogeomorphic engineers is controlled by both abiotic (e.g., physical habitat) and biotic variables (e.g., species interactions). (2) The zoogeomorphic effects of an organism are a result of the behavior, biomass (body size \* abundance) and life history of that individual. We build on previous models by explicitly considering the importance of organism behavior as a key control, not just on the magnitude, but also on the direction of zoogeomorphic effects (Figure 6). In contrast, we consider biomass and life history to be primarily controls on the magnitude of zoogeomorphic activity (over space and time respectively). (3) The activities of the organism are mediated by the abiotic environment. (4) Zoogeomorphic effects may modify habitat and species distributions through zoogeomorphic feedback (ecosystem engineering, Jones et al., 1994)

### 3 | UNDERSTANDING VARIABILITY IN INVERTEBRATE ZOOGEOMORPHOLOGY: A CONCEPTUAL MODEL

Both biological (e.g., behavior, body size, and abundance) and abiotic controls (e.g., grain size and hydraulic energy) are important to the zoogeomorphic effects of animals in rivers. Our conceptual model (Figure 5) considers the cycle of controls affecting the zoogeomorphic impact of an organism (following Moore, 2006). This model is particularly relevant to aquatic invertebrates because of the wide variety of behaviors with zoogeomorphic consequences reviewed here (Figure 6), but can be applied to all organisms.

#### 3.1 | Controls on organism distribution

The spatial and temporal distribution of organisms is evidently a primary control on their subsequent zoogeomorphic effects. Both physical habitat characteristics (particularly flow velocity and bed sediment type; Cummins & Lauff, 1969; Southwood, 1977; Statzner et al., 1988; Statzner & Higler, 1986) and biological processes (e.g., dispersal and competition; Murphy & Davy-Bowker, 2005) are important controls. However, the abundance of freshwater flora and fauna has reduced by 81% (1970–2012; WWF, 2016) and invertebrates are threatened by multiple pressures including habitat loss, pollution, invasive species, and climate change (Darwall et al., 2012; Strayer, 2006). This is concerning not only because of the intrinsic value of species, but also the loss (or alteration) of the ecosystem and zoogeomorphic services that they provide (Cardinale et al., 2012). Furthermore, invasive alien species (IAS) affect the distribution and activities of native zoogeomorphic taxa (e.g., mussels, Machida & Akiyama, 2013; caddisfly, and gastropods, Mathers et al., 2016; Chironomidae, Creed & Reed, 2004). Furthermore, of the most destructive IAS (as defined by the Global Invasive Species Database, 2020), 81% had the potential to directly affect geomorphology (Fei et al., 2014) and can achieve especially high biomass by escaping environmental and biological constraints present in their native ranges (Hansen et al., 2013; Harvey et al., 2011).



**FIGURE 6** Linking organism behavior traits to zoogeomorphic effects (see Box 1; Figure 5). Organism behavior has the potential to affect geomorphology via a number of specific mechanisms, which may destabilize (blue boxes) or stabilize sediment (orange boxes). Burrowing and locomotion biturbate and bioerode sediment (e.g., Mermillod-Blondin, 2011; Rice et al., 2019). Attachment to the bed surface may consolidate sediment via filtration and provide bioprotection (e.g., caddisfly filter feeding nets). Feeding activities may have different zoogeomorphic affects based on activity. Foraging may increase bioturbation (e.g., crayfish; Johnson et al., 2010 and stonefly; Statzner et al., 1996) while filtering removes sediment from the water column (e.g., Mussels; Tuttle-Raycraft & Ackerman, 2018). Both autogenic and allogenic construction are forms of bioconstruction and can provide bioprotection and biofiltration (e.g., caddisfly nets and mussel shells; Zimmerman & de Szalay, 2007)

### 3.2 | Organism controls: behavior, biomass and life history

We suggest that abundance and body size (biomass) and life history primarily influence the magnitude of a zoogeomorphic effect while the nature and direction of the effect (Box 1) is chiefly a result of organism behavior (Figure 5.2). This review has demonstrated the incredibly diverse range of behaviors exhibited by aquatic invertebrate taxa, which affect sediment stability or transport. Based on a comparison of zoogeomorphic research contained within this review we identify those behavioral traits with zoogeomorphic impacts (Figure 6), which facilitates a deeper understanding of how invertebrates modify their physical environment.

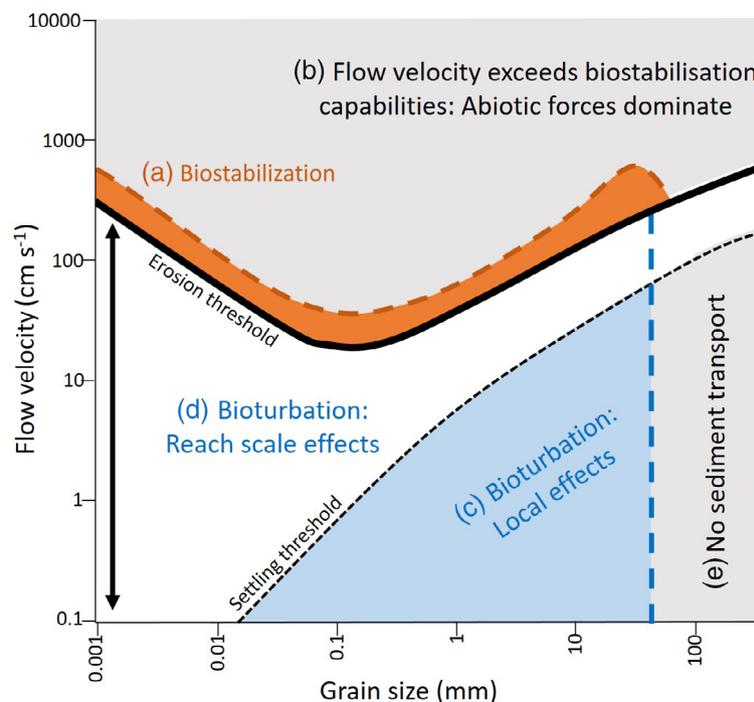
Behavioral or functional trait approaches have been used in biogeomorphology with success (e.g., for three individual invertebrates; Mermillod-Blondin et al., 2002, for vegetation; Schwarz et al., 2018; Tabacchi et al., 2019). This approach is particularly valuable for diverse organism groups such as freshwater invertebrates where zoogeomorphic research for all taxa individually is impossible, but many share behaviors and have similar zoogeomorphic effects (Albertson & Allen, 2015). However, it should be noted that organism behavior will vary not only between species, but also between individuals of the same species and from the same organism over time (e.g., due to life history). Invasive taxa may also change their behavior when moving out of their native range (Reader & Laland, 2003; Reznick & Ghalambor, 2001; Sol & Weis, 2019). Invasive species therefore represent a particular challenge in predicting potential geomorphic effects.

Body size and abundance primarily affect the magnitude of zoogeomorphic effects (Figure 5.2). Larger animals typically have larger individual effects, while the abundance or density of the organism affects the magnitude of effects observed at the population scale (Albertson & Allen, 2015). However, there are exceptions to both of these assumptions. First, larger individuals may be able to affect larger particles, and therefore organism size may also affect the zoogeomorphic mechanism as well as the magnitude (e.g., larger *Stenopsychidae* caddisfly larvae may stabilize larger sediment than smaller *Hydropsychidae*; Nunokawa et al., 2008; Takao et al., 2006). Second, increasing density of a zoogeomorphic organism does not always increase zoogeomorphic magnitude and may modify direction. For example, with increasing density of mussels (Widdows & Brinsley, 2002) and Polychaete worms (Friedrichs et al., 2000), populations reverse from having a destabilizing to a stabilizing effect.

The life history of taxa controls the timing of their zoogeomorphic effects (Figure 5.2). Zoogeomorphic behavior will change seasonally in relation to the lifecycle of invertebrate taxa, such as the transition from constructing filter nets and retreats to pupal cases by Hydropsychidae caddisfly larvae (Statzner et al., 2005). Furthermore, cohorts of small larvae in high densities transition to lower densities of larger larvae over time, affecting both density- and body size-driven effects. Consequently, consideration of biomass and life history alongside organism behavior is important to understand strength and mechanism of invertebrate zoogeomorphic effects (Figure 5.2).

### 3.3 | Environmental context: a gradient of geophysical energy

An important control on the magnitude of a zoogeomorphic action is the environmental context (Albertson & Allen, 2015; Moore, 2006). Freshwater habitats span a wide range of hydraulic and geomorphic environments, which mediate zoogeomorphic activity in different ways. We conceptualize fluvial habitats as a gradient from fast flowing rivers characterized by coarse particles and high geophysical power to slow flowing environments with fine sediment. This is a simplification because many sediment and hydrological factors not considered in this gradient influence zoogeomorphological effects, including near bed turbulence, sorting of sediment grains, water

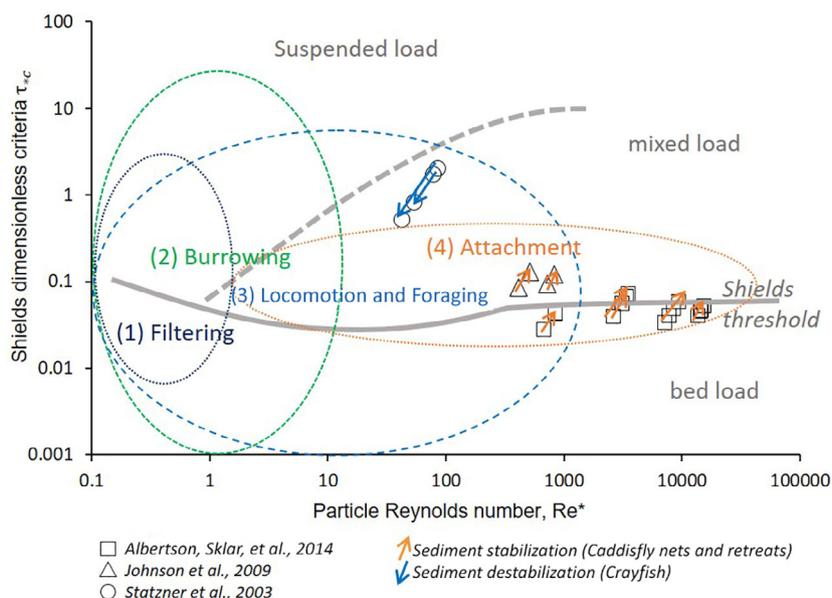


**FIGURE 7** Conceptual Hjulström (1935) curve modified to include the influence of zoogeomorphology. Fine grained sediments require high flow velocities to entrain due to cohesive bonds between grains (high erosion threshold), but once eroded require very little flow to remain entrained in the water column (low settling velocity). For coarser particles sizes (>0.1 mm), critical flow velocity and settling velocity increase with particle size. Plotted zoogeomorphic-adjusted flow velocity thresholds are a conceptual representation and have not been empirically quantified. (a) Biology increases the erosion threshold via biostabilization (e.g., Hydropsyche caddisfly nets increase flow velocity to erode 2–10 mm grains by 30%; Cardinale et al., 2004 and stabilize up to about 65 mm diameter sediment; Albertson, Sklar, et al., 2014). Microbes and aquatic macrophytes also increase the erosion threshold of clay, silt and sand particles (not reviewed here, but see Le Hir et al., 2007 in marine systems and Gurnell, 2014; Wharton et al., 2006 for aquatic vegetation). (b) Above the biostabilization threshold, high flow velocities break up stabilizing structures. (c) Bioturbation reduces the erosion threshold of sediment and is largely independent of flow velocity. However, when flow velocity is below the settling threshold of that sediment, sediment will only be moved locally (e.g., rolled by crayfish; grain size up to 38 mm; Johnson et al., 2010). (d) When the settling threshold is exceeded, bioturbated sediment will be transported downstream with larger scale impacts

worked grain structures (Rice et al., 2012), and the availability of specific grain sizes (Mason et al., 2019; Statzner & Dolédec, 2011). To understand the importance of zoogeomorphic engineers across gradients in hydraulic power and sediment size, we add biology to two fundamental concepts in fluvial geomorphology. Hjulström (1935) depicted the flow velocity required to entrain sediment (erosion threshold; Figure 7) and the flow velocity required to keep sediment entrained (settling velocity) for sediment of different sizes. Shields (1936) provides a nondimensional measure of entrainment threshold, widely used in studies of particle entrainment (Yang et al., 2019, Figure 8).

### 3.3.1 | Slow flowing rivers and lakes

Lakes and rivers with minimal flow velocity are typically characterized by fine grained sediments and low hydraulic conductivity within the sediment (Mermillod-Blondin & Rosenberg, 2006). In these conditions, the movement of sediment is important because of the strong effects on microbial and geochemical processes (Mermillod-Blondin, 2011). The effects of bioturbation are localized because there is insufficient hydraulic energy to transport sediment (Figure 7c). While slow flowing rivers may not have enough power to erode sediment from their bed or banks, they may have energy to transport very fine sediment with a low settling velocity bioturbated by organisms (Figure 7d). This is especially true for cohesive clay sediment because there is a large difference between the hydraulic energy required to erode and energy required to maintain transport, and so animals that facilitate the entrainment of fine sediments are



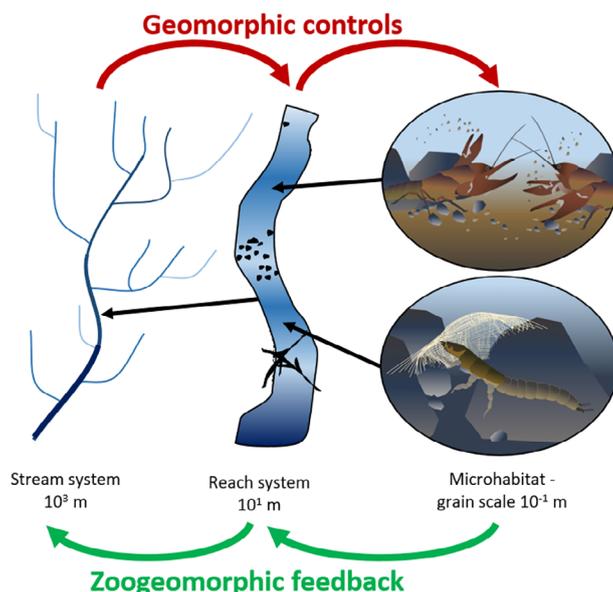
**FIGURE 8** Effects of aquatic invertebrates on the force required to entrain sediment, based on the empirical work of Shields (1936). Particle Reynolds number is  $Re^* = (u^*D)/\nu$ , where  $u^*$  is the shear velocity,  $D$  particle size, and  $\nu$  the kinematic viscosity of water. Particle Reynolds number can be interpreted as scaled particle size (Church 2006). Shields parameter is  $\tau_c^* = \tau_c / (\rho_s - \rho)gD$ , where  $\tau_c$  is the critical shear stress,  $\rho_s$  and  $\rho$  the density of sediment and water respectively and  $g$ , acceleration due to gravity. Shields threshold (based on the empirical work of Shields, 1936) and the threshold for sediment suspension (from Church 2006) in gray. Zoogeomorphic studies included in this review that considered the effects of invertebrates on critical shear stress are included. Studies must report either incipient shear stress or Shields values for both invertebrate treatments and controls. Surprisingly few studies consider critical shear stress with many measuring mass of sediment transported instead. Arrows indicate approximate increase and decrease in sediment stability between the mean value of the control and treatment with the largest difference. We assumed all sediment had a density of  $2,650 \text{ kg m}^{-3}$ . Values are approximate, as in some cases values had to be interpreted from graphs within these published articles. The environmental ranges of key zoogeomorphic behaviors (Figure 6) are conceptualized based on literature reviewed in this article. (1) Biofiltration only affects very fine sediment in suspension, (2) burrowing affects fine-medium grain sizes above and below the threshold for motion, (3) locomotion and foraging moves sediment across a wide range of grain sizes, (4) attachment consolidates sediment, which is only important above the threshold for motion. More research which considers changes to threshold shear stress due to taxa with different behaviors is required to quantify these groups. At higher  $\tau_c^*$  and  $Re^*$  it is expected that abiotic forces will dominate over biotic forces

important (Figure 7d). For example, clay particles eroded from river bed and banks by signal crayfish are transported downstream even during base flow (Rice et al., 2016). In slow flowing environments, there is little geophysical energy, and therefore biology can account for a substantial proportion of sediment transport.

### 3.3.2 | Fast flowing rivers

The directional flow of water downstream means that zoogeomorphic engineers that alter the exposure of sediment to erosive hydraulics at the sediment–water interface may be especially important. Furthermore, rivers with a mixed sediment size typically develop stabilizing grain structures, with coarse surface material “armoring” finer subsurface sediments (Church, 2006; Dietrich et al., 1989). This increases the hydraulic force required to transport surface grains and therefore expose the finer sediment beneath (Parker, 2008). Consequently, bedload transport in most rivers occurs rarely and sporadically but once surface grains are disturbed, rivers can then transport exposed fine sediment for longer. Invertebrate engineers can work with or against bed armoring. While small invertebrates only bioturbate fine material, biostabilizing invertebrates can modify entrainment of much coarser sediments. The silk nets and retreats of caddisfly larvae strung between gravel particles can further stabilize grain structures of gravel up to 65 mm in diameter (Albertson, Sklar, et al., 2014), increasing the force required to entrain protected grains beneath the surface (Albertson et al., 2019; Figures 7a and 8). However, at larger particle sizes the stabilizing effects of invertebrates will be dwarfed by the inertia of the stabilized particles themselves (Johnson et al., 2009).

In contrast, bioturbating taxa may destabilize the armored river bed surface itself or transport fine sediment through the armored layer onto the surface (Figure 1). Signal crayfish are able to move grains up to six times their own mass and destabilize grain structures (Johnson et al., 2010), and fighting signal crayfish in mesocosms reduced water-worked gravel imbrication by 37% after 6 h of exposure (Johnson et al., 2011). In rivers with armored beds, these actions would expose the finer material to erosion, reducing the threshold required to entrain sediment (Figure 8).



**FIGURE 9** Hierarchical scale of river systems, representing top down controls of abiotic geomorphology and bottom up controls of zoogeomorphology (Modified from Frissell et al., 1986). Geomorphic drivers influence the form and function of rivers from catchment scale (stream system) down to the microhabitat scale. Less well understood are the zoogeomorphic feedbacks which provide a reciprocal control on larger scale processes. For example, small scale locomotion and burrowing behaviors by crayfish supply fine sediment into the river channel at the reach scale, affecting sediment budgets for catchments, at least during baseflow (Rice et al., 2016). Individual nets and retreats of Hydropsychidae caddisfly stabilize sediment particles, resulting in stable patches of sediment at the reach scale (Albertson et al., 2019) but measuring the effects of stabilization at the catchment scale is yet to be achieved

## 4 | SCALE AND GUIDELINES FOR FUTURE RESEARCH

Scale is a substantial challenge for biogeomorphological research (Naylor et al., 2002). Fluvial processes propagate upstream and downstream (Ward, 1989), and therefore, fluvial geomorphology is typically considered at large spatial scales. However, biogeomorphology must consider the behavior of organisms, often in controlled environments, requiring work at much smaller scales (especially true for smaller animals). The focus of fluvial geomorphology on large scale processes may be one reason that zoogeomorphic research in rivers has chiefly been concerned with larger taxa, while understanding of the geomorphic importance of invertebrates comes largely from other disciplines, like ecosystem engineering and ichnotaxonomy (De Nadaï-Monoury et al., 2013; Mermillod-Blondin, 2011; Mermillod-Blondin & Lemoine, 2010; Savrda, 2019).

Research reviewed in this article has demonstrated that at small scales (Figure 9; microhabitat—grain scale) invertebrate organisms can have a wide range of zoogeomorphic effects (Figure 6). However, only limited research (e.g., Faller et al., 2016; Rice et al., 2019; Sanders et al., 2021; Wallace et al., 1993) has considered zoogeomorphology at the scale of river reaches to catchments, which is necessary to consider zoogeomorphic rates in context with abiotic sediment budgets (Figure 9; reach and stream scale). For example, Rice et al. (2016) recorded an annual cycle of the biotic and abiotic forcing of suspended sediment transport. Signal crayfish accounted for 32% of baseflow sediment, equivalent to 0.46%–1.46% of total annual sediment load (Rice et al., 2016). Wallace et al. (1993) reported that extermination of macroinvertebrates resulted in a 76% reduction of suspended inorganic sediments over a 6-year period in experimental North American streams. This was hypothesized to be a result of reduced invertebrate feeding, and thus a reduction in the rate of the breakdown of organic material (Wallace et al., 1993).

These larger scale studies usually consider bioturbation because sediment signals can more easily be detected and separated from abiotic processes. Signal crayfish are primarily active at night, allowing Rice et al. (2016) to measure crayfish bioturbation by recognizing diurnal cycles in sediment loads. Hassan et al. (2008) separated bedload transport due to Salmonidae spawning because this occurred at discharges well below those required for fluvial entrainment of sediment. Seismic signals (Dietze et al., 2020) and the disturbance of markers (Rice et al., 2019), tagged particles (Gottesfeld et al., 2004) and characteristic sediment (De Nadaï-Monoury et al., 2013) have also been used to measure bioturbation in situ in rivers (for benthic organisms see the review, Maire et al., 2008). Upscaling the effects of biostabilization is more difficult because it requires a measure of how much sediment would have moved in the absence of biology. Attempts to upscale the zoogeomorphic effects of net-construction by caddisfly larvae (Figures 3c and 4a) have included numerical modeling (Albertson, Sklar, et al., 2014; Tashiro et al., 2005), flume experiments, and extrapolation from field experiments (Johnson et al., 2009). Field flumes (Gibbins et al., 2010) may provide an important link between tightly controlled flume experiments and field realism (Statzner, 2012).

To determine the zoogeomorphic effects of invertebrates at larger scales requires first sufficient understanding of their impacts at the microhabitat scale (Figure 9) across the range of abiotic and biotic external controls present at the scale of interest (Figure 5). Upscaling may then be facilitated by advances in our ability to map zones of geomorphological process (e.g., Lorang et al., 2005; Scholl et al., 2021). Upscaling requires increased research to test the limits of zoogeomorphological effects. Models built on existing mesocosm and flume experiments are likely to overestimate zoogeomorphic effects because the latter are typically designed to consider conditions under which invertebrates are suspected to be important. Many zoogeomorphic engineers facilitate ecological (ecosystem engineers), as well as geomorphic change and many cohabiting taxa have contrasting geomorphic effects. Positive (Albertson et al., 2020; Tumolo et al., 2020) and negative (Katano et al., 2015) interactions in biotic communities are therefore likely to affect an organism's geomorphic impacts. Understanding community level zoogeomorphic effects is therefore a key area of future research.

## 5 | CONCLUSIONS

Darwin's (1881) book on sediment engineering by earthworms has been followed by extraordinary advances in our understanding of the effects of tiny invertebrates on physical processes and landscape development. While fluvial geomorphology has been slower to consider the zoogeomorphic effects of invertebrates than other disciplines, a diverse range of sediment engineering effects are documented for lotic invertebrates. This paper has reviewed zoogeomorphic

effects in rivers and provides a new traits based conceptual model and research framework to guide future research in lotic invertebrate zoogeomorphology. We hope that it will inspire deeper and wider research into the rates and mechanisms through which invertebrates affect sediment transport.

The directional flow of water in rivers allows lotic invertebrates to have far more widespread effects, contributing, if only marginally, to processes of landscape denudation (Figure 9). Invertebrates with zoogeomorphic behaviors are present in virtually every freshwater system. Furthermore, many invertebrate taxa are present year round, including those with terrestrial life stages (e.g., Hydropsychidae; Boon, 1979; Edington & Hildrew, 1995) and for many, their zoogeomorphic behaviors are conducted year round. This is in contrast to many well-researched zoogeomorphic taxa. Salmon, for example, primarily influence sediment dynamics during spawning season (typically November to February, Northern Hemisphere). Consequently, lotic invertebrates can have spatially and temporally widespread zoogeomorphic effects across a broad range of abiotic environments.

Sediment engineering by lotic invertebrates does not conform to traditional understanding of sediment transport in rivers. Even if the total mass of sediment bioturbated or stabilized does not contribute much to total annual bedload (e.g., signal crayfish 0.46%–1.46%, Rice et al., 2016), the zoogeomorphic impact may still be important. Fine sediment transported during base flow conditions is less likely to be flushed downstream and may have greater negative effects on water quality than that transported in floods. Furthermore, sediment transport in many rivers is dominated by sand sized sediment (Church, 2010; Leopold, 1992; Lisle, 1995), a size fraction that invertebrates are able to affect the transport of, both via bioturbation and biostabilization.

The importance of biology in rivers is gaining recognition in river management. Zoogeomorphic effects can be used to enhance river ecosystem services (e.g., beaver rewilding to restore biodiversity; Law et al., 2017), or to prioritize the conservation of species which usefully affect sediment dynamics or increase habitat diversity. This article has shown that invertebrates are not only essential to the ecological functioning of freshwaters (Wallace & Webster, 1996), but are also important sediment engineers with small scale effects which may be important at much larger scales. In contrast, invasive invertebrates are causing sediment problems (Albertson & Daniels, 2016a; Arce & Diéguez-Urbeondo, 2015). Remediating these negative effects requires understanding of the mechanisms of invertebrate zoogeomorphology.

The key challenges for future invertebrate zoogeomorphic research are (i) their taxonomic and behavioral diversity and (ii) upscaling from their individual effects to communities and wider spatial and temporal scales. Further consideration of invertebrate functional behaviors, as presented in this article, may provide a useful mechanism for generalizing between taxa.

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## CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

## DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study

## AUTHOR CONTRIBUTIONS

**Richard Mason:** Conceptualization; writing-original draft; writing-review & editing. **Harry Sanders:** Conceptualization; writing-original draft; writing-review & editing.

## ORCID

Richard J. Mason  <https://orcid.org/0000-0002-4571-7393>

Harry Sanders  <https://orcid.org/0000-0003-3031-2227>

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