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Invited review

Incorporating ecogeomorphic feedbacks to better understand resiliency in streams: A review and directions forward

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ABSTRACT

Decades of interdisciplinary research show river form and function depends on interactions between the living and nonliving world, but a dominant paradigm underlying ecogeomorphic work consists of a top-down, unidirectional approach with abiotic forces driving biotic systems. Stream form and location within the stream network does dictate the habitat and resources available for organisms and overall community structure. Yet this traditional hierarchal framework on its own is inadequate in communicating information regarding the influence of biological systems on fluvial geomorphology that lead to changes in channel morphology, sediment cycling, and system-scale functions (e.g., sediment yield, biogeochemical nutrient cycling). Substantial evidence that organisms influence fluvial geomorphology exists, specifically the ability of aquatic vegetation and lotic animals to modify flow velocities and sediment deposition and transport — thus challenging the traditional hierarchal framework. Researchers recognize the need for ecogeomorphic frameworks that conceptualize feedbacks between organisms, sediment transport, and geomorphic structure. Furthermore, vital ecosystem processes, such as biogeochemical nutrient cycling represent the conversations that are occurring between geomorphological and biological systems. Here we review and synthesize selected case studies highlighting the role organisms play in moderating geomorphic processes and likely interact with these processes to have an impact on an essential ecosystem process, biogeochemical nutrient recycling. We explore whether biophysical interactions can provide information essential to improving predictions of system-scale river functions, specifically sediment transport and biogeochemical cycling, and discuss tools used to study these interactions. We suggest that current conceptual frameworks should acknowledge that hydrologic, geomorphologic, and ecologic processes operate on different temporal scales, generating bidirectional feedback loops over space and time. Hydro- and geomorphologic processes, operating episodically during bankfull conditions, influence ecological processes (e.g., biogeochemical cycling) occurring over longer time periods during base-flow conditions. This ecological activity generates the antecedent conditions that influence the hydro- and geomorphologic processes occurring during the next high flow event, creating a bidirectional feedback. This feedback should enhance the resiliency of fluvial landforms and ecosystem processes, allowing physical and biological processes to pull and push against each other over time.

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1. Introduction

Decades of interdisciplinary research in fluvial systems demonstrates that river form and function depend on interactions between abiotic and biotic factors. A dominant paradigm underlying ecogeomorphic work consists of a hierarchy with abiotic forces driving biotic systems (Frissell et al., 1986; Thoms and Parsons, 2002). This top-down, unidirectional approach, implicit with the idea that macroscale factors (e.g., geology, climate) determine microscale geomorphological and ecological conditions, has resulted in significant gains in understanding fluvial systems, including aspects of energy budgets and nutrient cycling (e.g., Meyer and Edwards, 1990; Alexander et al., 2000; Peterson et al., 2001b; Mulholland et al., 2008). Still, this approach falls short in adequately explaining how biological systems influence geomorphological processes occurring in rivers, leading to changes in channel morphology, sediment cycling, and system-scale functions (e.g., sediment yield, nutrient cycling). Consequently, researchers have begun to include bidirectional feedbacks between ecological and geomorphological processes (Post et al., 2007; Allen et al., 2014; Julian et al., 2016) — ecogeomorphology.

With growing concerns about the integrity and resiliency of landscapes and ecosystems in the face of global change (NRC, 2010), the need to understand feedbacks between the top-down geophysical effects (e.g., hydrogeomorphic disturbance) on biota and the bottom-up biological effects on geophysical processes is pressing (Fig. 1; Allen et al., 2014). The geomorphic template of a stream is well known to govern abiotic habitat conditions, influencing species compositions of biological communities (Vannote et al., 1980; Frissell et al., 1986; Atkinson et al., 2012). This traditional framework has been advanced by including feedbacks among organisms, sediment transport, and geomorphic structure (Fisher et al., 2007; Corenblit et al., 2008; Riggsbee et al., 2013). This includes the ability of aquatic and riparian vegetation to modify flow velocity (Watson, 1987; Sand-Jensen, 1998; Gurnell and Petts, 2006) and sediment deposition (Sand-Jensen and Mebus, 1996; Sand-Jensen and Pedersen, 1999), and the ability of animals to stabilize and destabilize bed sediments (Statzner, 2012; Rice et al., 2016). We now know that biological systems influence channel morphology, sediment cycling, and system-scale functions (e.g., sediment yield, nutrient cycling), but these feedbacks between geomorphological and ecological processes have yet to be fully explored. Although we are aware that these feedbacks exist, they have been rarely assessed directly (Fisher et al., 2007; Allen et al., 2014), likely because of the different temporal scales that regulate these processes (Post et al., 2007). Moreover, we seldom think about how these feedbacks might ultimately govern the performance of key ecosystem processes, such as primary production or biogeochemical cycling. We argue here that biogeochemical cycling may be used as an indicator of system resiliency and is strongly regulated by feedbacks between the geomorphological and ecological systems. These fundamental ecosystem processes further influence the geomorphic structure of the system and, as such, represent the conversations that are occurring between geomorphological and biological systems.

2. Existing frameworks for understanding river form, communities, and ecosystem function

Rivers are complex systems involving a large variety of subsystems, including hydroclimatic, ecological, political, sociological, and geomorphic systems (Poff, 2014; Ashmore, 2015). A truly holistic framework for any given river, much less all rivers, is an ambitious charge, albeit worthy of pursuit. Here we emphasize the hydrological, geomorphological, and biological processes involved with the transfer of mass and energy. These processes produce the physical and chemical characteristics of rivers. As such, we review how their interactions have been conceptualized and reconceptualized to date.

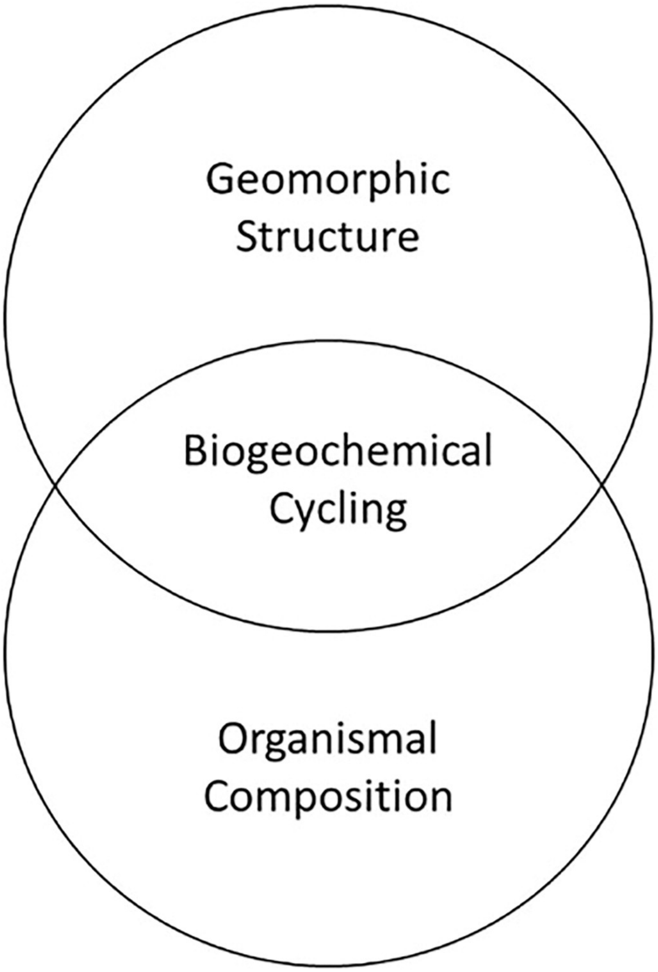

Fig. 1. The interface of the geomorphic structure of the fluvial system and the organisms that are supported interact to influence essential ecosystem processes that enhance the overall resiliency of these systems.

Early holistic frameworks set the precedent that the physical subsystems of rivers govern the spatial variability of biological systems. The River Continuum Concept (RCC; Vannote et al., 1980) described longitudinal changes in biological habitat as a consequence of variability in large-scale factors such as climate, hydrology, and geomorphology that cause access to biological resources to change over space. Given the emphasis the RCC placed on longitudinal gradients, subsequent conceptual models worked to integrate lateral exchanges between the channel and the riparian corridor and their implications for organisms to access ecological resources from extra channel environments, such as organic matter from floodplains. The Flood Pulse Concept (Junk et al., 1989) characterized floodplain and channel connectivity as a function of temporal changes in discharge. The Hyporheic Corridor Concept (Stanford and Ward, 1993) focused on the lateral exchange of groundwater between the floodplain and the channel, while also considering vertical exchanges between the channel and the hyporheic zone. Much of the work related to lateral connections and exchanges in riverine ecosystems focused on large, lowland, tropical rivers. The Flow Pulse Concept (Tockner et al., 2000) extended lateral connections to floodplains in upper and middle reaches of temperate rivers, emphasized the ecological implications of variable discharge below bankfull discharge conditions, and introduced the idea that spatial variability in water temperature creates floodplain habitat heterogeneity. Poole (2002) advocated the development of a subfield termed *fluvial landscape ecology* to unify distinct but parallel ideas (including the RCC, the Flood Pulse Concept, and the Hyporheic Corridor Concept) into one conceptual framework by applying a Hierarchical Patch Dynamics perspective. The Hierarchical Patch Dynamics approach divides fluvial landscapes into a hierarchy of *patches*, or landscape elements, which occur at different spatial scales. Processes within this framework can transcend spatial scales and consist of two groups. *Top-down* processes originate from large-scale phenomena (a flood, for example) that can affect components right down to the finest (patch) spatial scale and *bottom-up* processes occur at finer spatial scales but can lead to changes at the broader spatial scale, such as succession within ecosystems. Benda et al. (2004) proposed the Network Dynamics Hypothesis, which examines how river confluences mediate the effects of disturbance events such as floods and fires, explaining how habitat heterogeneity develops and changes over time and space. Thorp et al. (2006) also proposed amendments to the Hierarchical Patch Dynamics approach in their Riverine Ecosystem Synthesis model, which adds concepts of Functional Process Zones, akin to those previously described by Montgomery and Buffington (1998), and relates how Functional Process Zones regulate community structure as a function of their location in the river network and its ecoregional setting.

Although these general models are broad in scope, they all focus on geomorphological and/or hydrological processes as drivers of biological processes. Some recent attempts to conceptualize ecogeomorphic interactions identify how channel form and interacting processes influence species distributions and their effects on ecosystems (Riggsbee et al., 2013; Fei et al., 2014). Many different species that use rivers as habitat also have the potential to modify it, often called *ecosystem engineers* (Jones et al., 1994; Flecker, 1996). But their potential to do so is not equal across all species, nor do all environmental modifications made by organisms have the potential to alter the fluvial geomorphology of rivers. Fei et al. (2014) distinguished those organisms with the ability to modify geomorphic processes and landforms as *geomorphic engineers*. Based on the research conducted to date, some semiaquatic/terrestrial species (including beavers, cows, bison, and hippopotami) have greater potential to help determine channel morphology at larger spatial scales (valley segment), while most aquatic organisms have more potential to create localized channel morphology changes (Riggsbee et al., 2013). The overall effect of aquatic organisms on sediment transport seems to be small in comparison to conditions of sediment transport under high flow conditions and is related to organisms increasing the critical shear stress needed to entrain sediment (Riggsbee et al., 2013). Most of these observations, however, are confined to flume studies and individual species and bear further investigation under field conditions where organisms are modifying the environment as part of a community in a complex environment.

Here, we propose an integration of biophysical interactions and ecosystem function within existing ecogeomorphic frameworks to better understand and predict fluvial and biogeochemical changes in the face of projected land use and climate changes. We suggest that an enhancement of the current conceptual frameworks for understanding rivers is needed — one in which organisms experience and influence the behavior of fluvial systems and in which abiotic and biotic systems codevelop through interactions spanning temporal and spatial scales (Post et al., 2007). As the top-down effects of hydrology and geomorphology on organisms and ecosystems are relatively well known (Vannote et al., 1980; Stanford and Ward, 1993; Tockner et al., 2000; Poole, 2002; Benda et al., 2004; Thorp et al., 2006), we first review existing case studies that document how organisms influence hydrological and geomorphological processes. We then suggest an incorporation of the reciprocal feedbacks across geomorphic processes, biological entities and succession of communities, and ecological functions that are contingent on these ecosystem feedbacks into the existing conceptual frameworks (Fig. 2). Our objective is to explore how the dynamic coupling between biological traits and hydrogeomorphic processes produce dynamic feedback cycles that are contingent upon environmental characteristics and influence ecological processes that are indicators of ecosystem resiliency.

3. Geomorphic structure and biological effects on biogeochemical nutrient recycling

The biogeochemical cycling of nutrients is an essential ecosystem activity controlled by physical and biological processes and the various interactions and feedbacks that exist between them (Fig. 1; Minshall et al., 2000; Fisher et al., 2004; Gücker and Boëchat, 2004). Nutrients are essential for organismal growth and cycle between biotic and abiotic compartments of the ecosystem and thus strongly regulate the structure and function of ecosystems. Therefore, biogeochemical cycling rates may be used as an indicator of system efficiency and resiliency. Biogeochemical cycling in streams is thought to be controlled by the geomorphic structure (i.e., channel slope, stream width; Gücker and Boëchat, 2004), hydrology (i.e., water velocity, depth, transient storage; Valett et al., 2002), biotic activity (Hall and Tank, 2003), and the balance of nutrients in the ecosystem (i.e., ecological stoichiometry; Gomez-Velez et al., 2015). As a more integrative approach is required to understand the feedbacks between the physical template and organisms within streams, we argue that river biogeochemistry is a unified ecogeomorphic response variable because it incorporates geomorphological and ecological processes occurring across a range of spatial and temporal scales.

Biogeochemical cycling may be considered a measure of system resiliency as it incorporates the flux and storage of nutrients within systems. Nutrient spiraling incorporates the interplay between ecological and geomorphic processes to understand the transport and cycling of biologically active elements in streams (Newbold et al., 1982; Minshall et al., 2000; Ensign and Doyle, 2006). Nutrient spiraling length describes the distance an element travels as it completes a cycle between organic and inorganic forms. Operationally, the dimensions of nutrient spiraling are most often quantified by measuring a nutrients uptake length. Uptake length is the downstream distance a dissolved molecule travels before it is removed from the water column, which can occur through biotic assimilation, physical sorption, or transformation (Newbold et al., 1982). A large proportion of nutrient inputs within a stream can be assimilated by bacteria and/or algae and cycled through benthic microbial communities (Ensign and Doyle, 2006). Inorganic nutrients travel longer distances in streams prior to biological assimilation in comparison to terrestrial or lake ecosystems due to the unidirectional

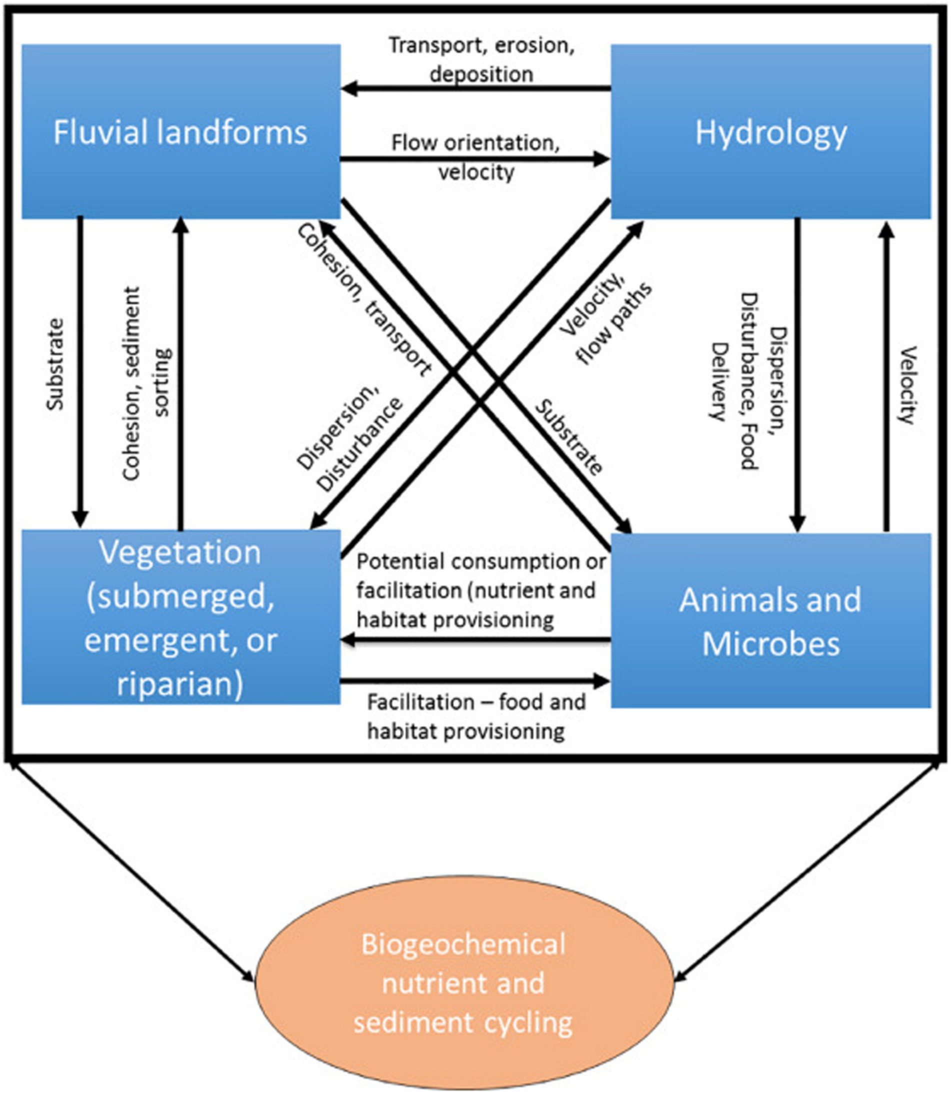

Fig. 2. The physical template (i.e., fluvial bedforms) and movement of water (i.e., hydrology) within rivers interact with each other and interact with the biological components of rivers (e.g., vegetation, microbes, and animals), creating a feedback among the structural components of the system. For example, the fluvial bedforms of the system influence the substrate composition and availability, while riparian plants and emergent vegetation may influence the cohesion and sorting of sediments within the system. Likewise, hydrology may influence the distribution of organisms, the delivery of food, and successional dynamics within communities. Collectively, these feedbacks with the river system influence biogeochemical and sediment cycling that feedback into the system and are essential processes.

transport of nutrients by streamflow. Yet, hotspots and hot moments of biological demand arise from a complex interaction between geomorphic structure, hydrology, and organismal abundance and activity. Furthermore, biological communities can indirectly influence nutrient cycling by altering sediment composition and compaction (e.g., mussels) and geomorphic structure (e.g., beavers). For example, as macrophytes, algae, and other vegetation become established in streams, benthic sediments can become finer and richer in organic matter, promoting microbial activity and shortening nutrient uptake length (Valett et al., 2002; Webster et al., 2003; Hill et al., 2010). As organisms colonize habitats and alter sediment dynamics and nutrient cycling, the integration of these actions can form ecogeomorphic feedbacks, altering nutrient spiraling length dynamics.

The alteration of sediment movement and deposition by plants and animals leads to consequential changes in biogeochemical cycling in the sediment (Forshay and Dodson, 2011; Turek and Hoellein, 2015). Biogeochemical processes such as denitrification and nitrification are heterogeneous in space and time, with disproportionately influential patches controlling nutrient processing and water quality in river systems (McClain et al., 2003; Tatariw et al., 2013). These patches are dependent on transport of nutrients to microbially active substrate along with a suite of proximal conditions to support biogeochemical processes. For example, enhanced denitrification is observed in individual hydrologic events like floods that connect the carbon-rich sediments and nitrate-rich water in floodplains (Forshay and Stanley, 2005), while seasonally stable habitats like aquatic weed beds provide the organic carbon, stability, and mineralized nitrogen to support substantial denitrification throughout the year (Forshay and Dodson, 2011). Understanding which habitats (or patches) support sediment accumulation, the proper redox conditions, microbial communities, and the controls on organismal distributions is necessary to better predict biogeochemical cycling across scales in rivers.

High densities of animals in fluvial systems can also create hotspots of enhanced nutrient cycling (McIntyre et al., 2008; Atkinson and Vaughn, 2015), potentially altering the stoichiometry of nutrients available in the system and changing nutrient spiraling dynamics (Small et al., 2009; Atkinson et al., 2013). The role of animals in modifying nutrient cycling has become increasingly accepted as an important influence on ecosystem function in aquatic systems (Vanni and Layne, 1997; Vanni, 2002). Animals sequester elements in their body tissues, transport them to new locations through their movements, release (or recycle) them via excretion and egestion, and thus hold the potential to significantly alter the availability and stoichiometry of nutrients within a stream or river (Vanni et al., 2002; Vanni et al., 2013). The recycling of nutrients by animals (McIntyre et al., 2008; Atkinson and Vaughn, 2015) can stimulate the growth of benthic biofilms (enhancing nutrient uptake; Atkinson et al., 2014b; Childress et al., 2014), alter the community composition of benthic algae (Allen et al., 2012; Atkinson et al., 2013), and lead to greater densities and different assemblages of aquatic insects (Vaughn and Spooner, 2006; Rantala et al., 2015). Biogeochemical hotspots may lead to greater food web connectivity and production in streams. Whether this could then feedback to influence ecosystem processes and geomorphic structure is a compelling research question (Gerbersdorf et al., 2008).

4. Case studies

A considerable body of literature demonstrates the ability of riparian and aquatic organisms to alter sediment storage and transport rates (Fritz et al., 2004; Allen and Vaughn, 2011; Riggsbee et al., 2013; Julian et al., 2016). Furthermore, particular channel morphologies are known for altering nutrient transformations in streams (Triska et al., 1993; Fisher et al., 1998, 2007). Few studies, however, have merged the ideas to determine the large-scale abiotic and smaller-scale biotic controls, including benthic organisms, influencing sediment transport and ecosystem processes and their feedback.

Virtually all sediment is inhabited by organisms ranging in scale from microscopic organisms (e.g., bacteria, fungi, algae) to macroscopic organisms (e.g., tree and macrophyte roots, bivalves). The geomorphic structure and hydrology of the system control the distributions of these organisms along the river longitudinal and transverse gradients. We propose that the cumulative organismal effects on geomorphic structure and their interactions with the abiotic environment strongly influence ecosystem processes, creating feedbacks to the structure and functioning of the abiotic and biotic components of the stream. The biotic contribution of organisms to sediment movement and content is complex. Benthic organisms can alter sediment dynamics by changing the hydrodynamic conditions at the sediment surface, as well as the structure and texture of the sediment. Aquatic vegetation consolidates sediment, influences channel form, and functions as food and habitat for animals in stream ecosystems. Thus, emergent and riparian vegetation can have considerable direct and indirect effects on channel processes (Hynes, 1975). The species composition and abundance of macroinvertebrates, fish, reptiles, amphibians, and even mammals (e.g., muskrats) can also greatly alter sediment transport and nutrient cycling within river systems. The role of this functional diversity and the traits represented (e.g., body size, life history) is essential for understanding feedbacks between the ecological and geomorphological systems. The predominant view governing conditions for sediment erosion, deposition, and transport is that bankfull discharge events are, in most cases, the same as the effective discharge and as such, strongly influence sediment transport and channel form. Bankfull events are also important in at least partially resetting biological conditions (depending on the taxa considered) and altering the course of successional dynamics in stream systems, which can alter community structure and resulting ecosystem processes over time (Poff et al., 1997; Townsend et al., 1997; Doyle et al., 2005; Bertrand et al., 2009; Parker and Huryn, 2011). A singular focus on moderate bankfull events, the effective discharge (Wolman and Miller, 1960), however, neglects important changes occurring during base-flow periods that help determine the potential for geomorphic work (sediment erosion, deposition, and transport) to be accomplished during less frequent, high discharge events (Doyle, 2005; Doyle et al., 2005). Additionally, the annual, seasonal, monthly, and weekly durations of bankfull discharge events are short in comparison to base-flow periods, in which organisms have a larger effect on important geomorphic (e.g., feeding and spawning activities, burrowing; Watters et al., 2001; Moore et al., 2007; Johnson et al., 2011) and ecosystem processes (e.g., such as biogeochemical nutrient cycling; Atkinson and Vaughn, 2015; Atkinson et al., 2017), which can interact (Moore et al., 2007). Here we outline some examples of organisms that are important drivers of geomorphic processes and likely interact with these processes to have an impact on an essential ecosystem process, biogeochemical nutrient recycling.

4.1. Riparian vegetation

Geomorphic processes, such as channel migration and flood duration, frequency, and intensity are well known to influence riparian plant distributions. Flood duration and groundwater availability can influence riparian plant community types (Hupp and Osterkamp, 1996; Lite and Stromberg, 2005), and stream migration rates can influence the density of riparian forests (Meitzen, 2009). But riparian plants can also influence geomorphic processes in fluvial systems by modifying channel size (Anderson et al., 2004; Constantine et al., 2009), enhancing trapping of sediments and reducing erosion (Julian and Torres, 2006), and as producers of large amounts of woody biomass that can itself modify physical forces imbued on streambanks by moving water (Hart, 2003; Julian et al., 2011), while also conferring physical strength to the soils they are embedded in (Table 1, Fig. 3A). These effects can lead to riparian vegetation having substantial effects on the processes shaping fluvial landforms.

There are three major processes that control the retreat or migration of streambanks in fluvial landforms: subaerial processes, fluvial erosion, and geotechnical erosion (Lawler, 1995; Julian et al., 2016). Riparian vegetation can play a role in each of these three processes (Thorne, 1990; Julian et al., 2016). Subaerial processes are climate-driven effects that reduce soil strength, making it more erodible, and include soil piping, shrink-swell, and freeze-thaw processes (Thorne, 1982). Riparian vegetation alters streambank soil moisture and temperature regimes, creating microclimates that influence subaerial processes and thus modify their associated effects on soil erodibility (Wynn and Mostaghimi, 2006). Fluvial erosion is the detachment, entrainment, and removal of soil particles or aggregates by hydraulic forces (Julian and Torres, 2006). Riparian plant roots modify this process by increasing the critical shear stress required to initiate sediment motion and physically trap sediment (Wynn et al., 2008). Aboveground riparian vegetation can also reduce fluvial erosion during bankfull flow events, as the physical structure of plant trunks, stems, and branches modifies near-bed hydraulic forces in ways that reduce shear stress near the boundary (Hopkinson and Wynn, 2009). Finally, geotechnical erosion (also referred to as bank failure) occurs when stream banks become unstable and collapse. Riparian vegetation impedes and promotes this process. Large woody roots can mechanically reinforce the streambank soil matrix, providing structural reinforcement that prevents stream bank collapse (Simon and Rinaldi, 2000; Simon and Collison, 2002). Finally, the weight of vegetation is thought to promote bank collapse via mass wasting (Thorne, 1990), though studies have shown that this magnifying effect is weaker than the effects of mechanical reinforcement that reduce bank failure (Abernethy and Rutherfurd, 2000).

Studies in this area have generally focused on the effects of single species or general plant types (i.e., grasses vs. trees), with much less investigation of how riparian plant communities (as multiple, interacting species) modify physical processes like streambank erosion (Allen et al., 2014). Results from biodiversity and ecosystem function (BEF) studies in ecology have shown that the species richness of plant communities increases their ability to convert belowground inorganic resources to biomass (Balvanera et al., 2006; Cardinale et al., 2006, 2011). These results also suggest that riparian plant biodiversity could influence physical processes such as erosion. Indeed, some preliminary work supports this hypothesis. In an experiment using artificial stream banks and herbaceous vegetation, Allen et al. (2016) found that more diverse plant communities led to more erosion resistant soils than

Table 1
Summary of the geomorphological and biogeochemical effects of representative aquatic taxa, as discussed in the "Case studies" Section.

Example	Geomorphological effects	Biogeochemical effects
Riparian vegetation	Regulates channel size (Anderson et al., 2004; Constantine et al., 2009) Roots retain soil and reduce erosion and bank failure (Julian and Torres, 2006) Major source of large woody debris in channel (Hart, 2003; Julian et al., 2011)	Canopy regulates input of energy to stream system (Kiffney et al., 2004; Cory and Kaplan, 2012) Soil retention leads to reduced nutrient load to stream system during runoff events (Schlesinger et al., 1996) Large woody debris can create hotspots of high organic matter and biogeochemical processes (Lazar et al., 2014)
Emergent macrophytes	Alter channel hydraulics (Dodds and Biggs, 2002; Fritz and Feminella, 2003; Wharton et al., 2006) Modify channel roughness by altering flowpaths (Madsen et al., 2001; Vaughn and Davis, 2015) Increase sediment deposition (Watson, 1987; Sand-Jensen, 1998; Fritz et al., 2004)	Assimilation shortens nutrient spiraling lengths and provides bottom-up provisioning of nutrient to the local food web (Eriksson, 2001) Increased sediment deposition can create hotspots of biogeochemical activity (Forshay and Dodson, 2011; Tall et al., 2011)
Algae and biofilms	Increases sediment cohesion (Paterson, 1997; Black et al., 2002) Increases erosion threshold at low flow velocities (Albertson and Allen, 2015; Gerbersdorf and Wieprecht, 2015)	Nutrient uptake decreases nutrient spiraling lengths (Martí et al., 1997; Hill et al., 2010) Biofilms provide bottom-up provisioning of nutrients to the local food web (Kobayashi et al., 2011; Eggert and Wallace, 2007)
Mollusks	Shells and shell aggregations contribute heterogeneity to benthic sediments (Gutierrez et al., 2003; Strayer and Malcom, 2007) Biodeposition by suspension-feeding bivalves alters physical and chemical characteristics of benthic sediments (Wotton and Malmqvist, 2001; Joyce et al., 2007) Freshwater mussels facilitate sediment cohesion through excretion and biodeposition (Paterson, 1997; Black et al., 2002) Burrowing behavior in mussels increases sediment transport and erosion (Allen and Vaughn, 2011; Johnson et al., 2011)	Dense, specious aggregations of freshwater mussels alter nutrient limitation and increase abundance of biofilm (Spooner and Vaughn, 2006; Atkinson et al., 2013) Invasive freshwater bivalves foster necessary conditions to stimulate nitrogen removal via denitrification (Bruesewitz et al., 2006; Bruesewitz et al., 2008; Turek and Hoellein, 2015)
Crustaceans	Bioturbation by crayfish (i.e. walking and tail flips) increase sediment transport (Statzner et al., 2000) Crayfish burrows destabilize bank sediments, leading to bank failure and alteration of channel morphology during high flow events (Harvey et al., 2011) Crayfish ingest fine sediment when feeding, reducing fine sediment accrual during base-flow conditions (Creed and Reed, 2004; Helms and Creed, 2005)	Excretion by high denisties of shrimp can account for up to 21% of N uptake and 0.5% of P uptake (Benstead et al., 2010)
Aquatic insects and worms	Many aquatic insects spin silk to bind sediment particles, making sediments more resistant to entrainment (Johnson et al., 2009)	Burrowing aquatic insects and tubificid worms create microenvironments able to sustain nitrogen removal via denitrification (Nogaro and Burgin, 2014)
Fish	Spawning fish that build nests in benthic sediments increase bed roughness (Hassan et al., 2015), suspend fine sediments (Moore et al., 2004), and initiate large-scale sediment movement (Gottesfeld et al., 2004; Hassan et al., 2008) Bottom-feeding fish ingest fine sediments, reducing fine sediment accrual during base-flow conditions (Power, 1990; Flecker, 1996; Flecker, 1997) Bottom-feeding fish also disrupt sediments while searching for prey, reducing critical sheer stress in benthic sediments (Statzner et al., 2003; Statzner and Sagnes, 2008)	Fish aggregations lead to biogeochemical hotspots, with collective excretion reducing nutrient limitation (McIntyre et al., 2008)
Aquatic mammals	Beaver dams completely alter an ecosystem, turning a stream into a series of wetlands connected by streams (Jones et al., 1994; Webb and Erskine, 2005) Hippopotami trails and movement lead to the development of new channels (McCarthy et al., 1998)	Beavers enhance sediment trapping, which also traps standing stocks of chemical elements and enhance production of methane (Ford and Naiman, 1988; Naiman et al., 1994) Hippopotami inputs via excretion and egestion are important resource vectors of C and N from terrestrial to aquatic habitats (Subalusky et al., 2015)

single species treatments. Furthermore, these results were strongest when mixing species comprising different functional groups (i.e., legumes and nonlegumes; Allen et al., 2016). These results mirror the results of another study that found reduced soil erosion in more diverse experimental treatments when manipulating the biodiversity of herbaceous vegetation on a simulated dike (Berendse et al., 2015). Finally, some work suggests that these patterns can be observed in natural conditions in the field. In an investigation of stream channel migration rates using historical aerial photography, Allen et al. (in review) found that increased woody plant diversity indirectly reduced stream bank migration rates across 38 sites in three rivers in Michigan, USA, mediated through direct effects on stem density. This indicates that sites with more tree species are more abundant, which presumably increases root biomass and reduces soil erodibility of stream banks.

The role of riparian plants on geomorphological processes extends well past their lifetime. Mortality of riparian vegetation is a result of a variety of natural and human-induced processes — including fire (Jones et al., 2011; King et al., 2013), disease (Evans et al., 2012; King et al., 2013), debris flows (May and Gresswell, 2003), landslides (Wohl et al., 2009), ice storms (Kraft et al., 2002), and timber harvest (Gomi et al., 2001; Hassan et al., 2005; Magilligan et al., 2008) — and is associated with increased input of large woody debris in rivers. The effects of large woody debris in river channels have been intensely studied given its well-established ability to directly modify river channel morphology, biodiversity, and ecosystem processes (Benke et al., 1985; Abbe and Montgomery, 1996; Hilderbrand et al., 1997). The presence of large woody debris within a fluvial system initiates streamflow deflection, which can alter channel morphology and sediment and nutrient dynamics in a variety of ways, including increasing localized erosion (Keller and Swanson, 1979; Daniels and Rhoads, 2003), increasing the formation of pools (Keller and Swanson, 1979) and woody steps that trap sediments (Megahan and Nowlin, 1976; Swanson and Lienkaemper, 1978; Megahan, 1982; Swanson and Fredriksen, 1982), decreasing channel gradient (Heede, 1975; Hogan, 1987), increasing bankfull depth and bankfull width (Hart, 2003), and increasing nutrient storage (Thompson, 1995) and uptake (Valett et al., 2002).

Riparian vegetation can also influence biogeochemical cycling, mainly through a combination of indirect physical processes (e.g., sediment retention, temperature changes) and direct uptake of nutrients. Riparian vegetation buffers a stream by reducing nutrient loads coming from terrestrial systems during runoff events. Riparian vegetation width is generally positively related to nutrient retention and removal (Naiman and Decamps, 1997; Mayer et al., 2007; Hoffmann et al., 2009). Furthermore, the sediments associated with

Fig. 3. Panel highlighting some of the organisms discussed in our case studies: (A) riparian vegetation along a streambank; (B) emergent macrophytes, *Justicia americana*; (C) biofilm composed of mix of autotrophic and heterotrophic microbes; and (D) stream-dwelling animals, including freshwater mussels (*Amblema plicata* pictured).
Photographs by C.L. Atkinson.

riparian vegetation typically have higher organic matter, nutrient content (Schlesinger et al., 1996), and microbial biomass (Gallardo and Schlesinger, 1992) than interspace sediments, which can facilitate productivity. Thus, processes that facilitate the establishment of riparian vegetation ultimately contribute to nutrient uptake and retention. This generates a positive feedback in which tree establishment reduces sediment transport and alters flow path configuration and landform construction, promoting hydrologic and nutrient retention in vegetated areas further (Hupp and Osterkamp, 1996; Corenblit et al., 2008; Dosskey et al., 2010). Trapped riparian sediments can also act as biogeochemical hotspots, removing nutrients and further reducing the influx of reactive nutrients entering a system over time (Vidon et al., 2010). The positive feedbacks associated with a stable riparian buffer contribute to resilience of stream systems, allowing a system to return to its previous state following a disturbance.

Riparian vegetation also regulates the energy available to a stream, influencing energy inputs in the form of light (Kiffney et al., 2004) and organic carbon (Cory and Kaplan, 2012). Light is a first-order control on stream ecosystems, as it drives primary production in benthic and pelagic realms (Julian et al., 2011) and alters the availability of autotrophic and heterotrophic resources to primary consumers (Collins et al., 2016). As stream morphology changes, so does the balance of heterotrophy and autotrophy, driving changes in food-web structure and nutrient spiraling (Vannote et al., 1980; Dodds, 2007). Riparian canopy cover is generally densest at the headwaters of a stream, where light penetration is lowest and carbon loading is highest. This results in a lower proportion of production relative to respiration. In downstream reaches, light penetration increases and allochthonous carbon loading per unit volume decreases (Vannote et al., 1980; Lamberti and Steinman, 1997). In-stream primary production leads to the assimilation of dissolved inorganic nutrients (see Algae and biofilms Section below), which are then made available to local food webs, reducing nutrient spiraling length. Detrital matter (i.e., leaf litter, wood debris) originating from riparian vegetation is also an important resource for stream consumers and is often transported to areas where proper geomorphological factors (i.e., bedform, streamflow) and nutrient concentrations foster the microbial biomass necessary for breakdown of detritus and dissolved organic carbon. Dissolved organic carbon is utilized by heterotrophic bacteria for growth, and its subsequent breakdown contributes to stream metabolism and biogeochemical cycling of nitrogen. Dissolved organic carbon is a key compound in cellular respiration, which promotes nitrification and denitrification when respiration occurs in aerobic and anaerobic environments, respectively (Strauss and Lamberti, 2002).

The influence large woody debris has on biogeochemical cycles in streams are similar to those exerted by riparian vegetation, as large woody debris stimulates sediment retention and buildup of organic matter within the stream (Valett et al., 2002; Dosskey et al., 2010). Over time, the buildup of sediment and organic matter upstream of large woody debris creates a somewhat pseudolentic environment, capable of fostering biogeochemical processes such as denitrification (Lazar et al., 2014). Also, the decay of woody debris and associated organic matter buildup can result in an increase of dissolved organic carbon entering the system, fueling bacterial productivity (Sabater et al., 1993; Meyer, 1994; Cole et al., 2006). Large woody debris also creates habitat in the form of regeneration sites for seedlings, as well as lead to the construction of habitat for fish and invertebrates (Wallace and Benke, 1984; Benke et al., 1985), increasing the complexity of geomorphic and biotic conditions (Naiman et al., 1999; Collins et al., 2012). This increase in channel complexity and primary and secondary production can have interactive effects on biogeochemical cycling that enhances uptake dynamics and increases storage.

4.2. Macrophytes

Aquatic plants are well known to modify hydraulics (Dodds and Biggs, 2002; Fritz and Feminella, 2003; Wharton et al., 2006), trap fine sediments (Sand-Jensen, 1998; Koetsier and McArthur, 2000), and alter nutrient transfer rates (Table 1; Forshay and Dodson, 2011; Julian et al., 2011; Tall et al., 2011). While emergent macrophytes modify stream habitats through promoting sedimentation, retaining organic matter, and reducing local current velocities (Sand-Jensen, 1998; Koetsier and McArthur, 2000; Madsen et al., 2001; Dodds and Biggs, 2002; Asaeda et al., 2010), little is known about how these patches influence streambed formation, reach morphology, and streambed stabilization. Deceleration of velocity within aquatic plant patches can result in accelerated velocities around plant patches to maintain downstream discharges (Sand-Jensen, 1998; Madsen et al., 2001), thus the impact of macrophytes are patch-dependent. Furthermore, as aquatic vegetation grows, stream hydraulic roughness is modified (Watson, 1987). For example, *Justicia americana* (common name: American water-willow; Fig. 3B) is a common emergent macrophyte in North American streams with a rhizomatous growth form. *Justicia americana* patches increase substratum stability (Fritz and Feminella, 2003; Fritz et al., 2004), alter flow velocity (Vaughn and Davis, 2015), and lead to greater sediment deposition (Fritz et al., 2004). Likewise, the accumulation of fine sediments within the channel associated with patches of algae and macrophytes and positive feedback processes that reinforce this accumulation can alter the form of reticulate flow networks in stream ecosystems. While the role of macrophytes in altering sediment transport and hydrology are complex, in general, they reduce flow velocities within their patches while enhancing flow velocity outside their patches, enhancing sediment deposition and stability, and modifying channel roughness (Madsen et al., 2001; Vaughn and Davis, 2015). These shifts in flowpaths and sediment accumulation can lead to varying rates of nutrient retention and processing.

Aquatic macrophytes play an important role in biogeochemical nutrient cycling in aquatic systems through a variety of physical and biological processes. As emergent aquatic macrophytes stabilize and trap sediments (Watson, 1987) and alter flow pathways (Sand-Jensen, 1998; Vaughn and Davis, 2015), they can lead to greater nutrient retention and hotspots of biogeochemical activities in rivers (Schulz et al., 2003; Forshay and Dodson, 2011; Tatariw et al., 2013). Collectively, emergent macrophytes are stable habitats that provide organic carbon and sediment stability, which are known to lead to the promotion of denitrification and nitrification (Forshay and Dodson, 2011; Tall et al., 2011). Furthermore, through the uptake of nutrients in the sediment and water column, macrophytes store nutrients in their tissue and make them available to the food web. Macrophytes are often colonized by algae, bacteria, and aquatic insects (Eriksson, 2001; Wharton et al., 2006; Hempel et al., 2009), leading to greater habitat heterogeneity, productivity, and higher denitrification rates (Eriksson, 2001). The provisioning of nutrients into tissue biomass and bottom-up provisioning to the food web by macrophytes shortens nutrient spiraling length and can increase system productivity, while the enhancement of denitrification zones results in a loss of N from the system. Thus, the inclusion of macrophytes into an ecogeomorphic framework will improve our understanding of system structural and process-based heterogeneity.

4.3. Algae and biofilms

Benthic algae, fungi, and bacteria embedded within a polysaccharide matrix (hereafter biofilms; Fig. 3C) are essential features of rivers that perform important ecosystem processes. These processes include transferring energy to higher trophic levels as the base of the food web and the uptake of nutrients that would otherwise continue to travel downstream (Battin et al., 2003b; Grabowski et al., 2011; Gerbersdorf and Wieprecht, 2015). Geomorphic structure and hydrologic routing indirectly influences broad-scale variation in biofilm distributions and densities through controlling the delivery of potentially limiting resources (e.g., nutrients; Jones and Mulholland, 1998; Dent et al., 2001; Hill et al., 2010). Watershed and channel morphology alter biofilm distribution and activity through effects on flow and water residence time (Battin et al., 2003a; Jordan et al., 2003; Wollheim et al., 2008) and light regime and productivity (Young and Huryn, 1996; Julian et al., 2008; Atkinson and Cooper, 2016).

Biofilms have interactive effects on sediment transport and flow dynamics that may accumulate to influence channel morphology. The presence of autotrophic and heterotrophic biofilms in streams alters the transport and deposition of particles (Dodds and Biggs, 2002). Biofilms are ubiquitous in stream ecosystems and comprise important physical structures that significantly mediate the erosive response of sediment particles to hydrodynamic forcing in streams (Paterson, 1997; Lubarsky et al., 2010; Gerbersdorf and Wieprecht, 2015). Laboratory and field studies have demonstrated that algae and biofilms increase erosion thresholds and decrease erosion rates of cohesive and noncohesive sediment by physically binding sediment grains (i.e., adhesion), creating a pliant structural matrix, and reducing boundary layer roughness (see reviews in Paterson, 1997; Black et al., 2002). Studies have shown strong positive correlations between erodibility and chlorophyll-*a*, a proxy for photoautotrophic microbial community abundance that includes diatoms and cyanobacteria (Blanchard et al., 2000; Tolhurst et al., 2003; Gerbersdorf et al., 2008). Furthermore, biofilms are known to produce extracellular substances that can bind particles together, but their role as ecosystem engineers has not been well studied (Grabowski et al., 2011; Vignaga et al., 2013; Albertson and Allen, 2015). A recent meta-analysis showed that biofilms reduce erosion and can have as large of an impact on sediment transport as much larger organisms, such as fish and crayfish for discharges ranging from <1 to 7 $m^3\ s^{-1}$ (Albertson and Allen, 2015). Thus, more work is needed to understand the interactive roles of biofilms, animals, and nutrient recycling on sediment dynamics and channel form.

Biofilms play a critical role in biogeochemical cycling as they mediate the recycling of nutrients from inorganic to organic forms (Falkowski et al., 2008). Biofilms can influence biogeochemical cycling through direct uptake and through the modification of the sediments. Nutrient spiraling uptake lengths and velocities have frequently been used to represent nutrient retention and overall activity in stream ecosystems (Newbold et al., 1981; Peterson et al., 2001a; Valett et al., 2002). Overall stream heterotrophic and autotrophic demand is a strong indicator of nitrogen uptake (Webster et al., 2003). Previous work has documented that biofilm abundance strongly influences nutrient spiraling length and uptake velocity in streams (Martí et al., 1997). In a multibasin study, Hill et al. (2010) showed that geomorphological attributes (i.e., wetted width, stream depth, slope, median grain size) and biofilm activity correlated with the uptake velocities of ammonium and phosphorus. Arnon et al. (2007) showed that hydrologic conditions structured algal biofilm communities that led to differential microbial communities and denitrification rates. These examples show that the interaction between channel form and the biological community strongly influences biogeochemical cycling and has a bottom-up effect on sediment transport as the biofilm community is being produced. Furthermore, as these nutrients are taken up by biofilms, they are transferred to higher trophic levels via ingestion (Eggert and Wallace, 2007; Kobayashi et al., 2011), some of which is remineralized into soluble nutrients by consumers via excretion (Vanni, 2002), leading to a feedback between biofilm communities and benthic consumers (Herren et al., 2017).

4.4. Animals

Animals have long been a focal point in studies of how organisms modify their physical environment as *ecosystem engineers* (Jones et al., 1994). Indeed, some classic examples of ecosystem engineers include stream dwelling organisms, such as beaver (Wright et al., 2002), fish (Flecker, 1996), and aquatic insects (Wotton et al., 1998); studies that are now being revisited in an ecogeomorphologic context (Statzner, 2012; Albertson and Allen, 2015). Stream animals have been shown to influence geomorphologic processes in two fundamental ways: either producing some type of physical structure, which then influences flow velocity or sediment transport, or by physically interacting with sediment through different behaviors that affect sediment cohesion and consolidation (Riggsbee et al., 2013). Finally, animals are now known to have very strong effects on biogeochemical processes, recycling nutrients through ingestion, digestion, and egestion (Table 1).

4.4.1. Physical structure

Animals can produce physical structures that influence geomorphologic processes by using materials that already exist in the environment activities, by producing their own materials through biological processes, or a combination of both (Vaughn and Hakenkamp, 2001; Statzner et al., 2003; Riggsbee et al., 2013). The first mechanism, where animals only use existing materials to create some type of physical structure, is best typified by the well-known dam-building behavior of beavers (Jones et al., 1994). Beavers build dams from trees and mud, turning flowing stream reaches into slow-moving pools, essentially creating wetland habitat patches throughout the stream network. This influences ecological (Wright et al., 2002, 2004) processes, changing plant species distributions such that wetland taxa persist in places they would otherwise be absent. But beaver dams also affect sediment dynamics in streams, storing sediments upstream and increasing the elevation of the channel beds (Pollock et al., 2007; Curran and Cannatelli, 2014; Levine and Meyer, 2014). While the geomorphologic effects of the beaver are notable, examples of other animal species using solely external materials to produce physical structure are rare.

Most animals that produce physical structure use materials produced by biological processes (often referred to as *biogenic structure*), which can have strong impacts on stream geomorphology. In some cases, this physical structure alone can influence ecological and geophysical processes, even long after animals die. Perhaps the best example of this phenomenon is the production of shells by freshwater mollusks (Gutierrez et al., 2003). Shells and shell aggregations can introduce complexity and heterogeneity into benthic environments, which are thought to affect near-bed turbulence patterns in ways that could affect sediment transport (Black et al., 2002). Dense aggregations of mussels are estimated to produce a great deal of shell material that persists upon the death of the animal, making them capable of producing >10 kg spent shell m^{-2}, which becomes incorporated into the local streambed sediment matrix and/or transported downstream (Strayer and Malcom, 2007).

Finally, animals can also influence geomorphologic processes by producing physical structure through a combination of existing and biologically produced materials. Suspension-feeding animals consolidate sediments by feeding and the creation of feces and pseudo-feces (Wotton and Malmqvist, 2001; Moore, 2006). Their feeding byproducts (un-, partially, or completely digested material) can combine with fine, suspended sediment and mucous to create particle pellets that subsequently become part of the bedload (Wotton and Malmqvist, 2001; Joyce et al., 2007). Freshwater mussel filter-feeding enhances sedimentation and redistribution of particles into the substrate that might otherwise have been transported downstream, leading to changes in the textural and chemical characteristics of sediments generally referred to as biodeposition (Wotton and Malmqvist, 2001; Wotton et al., 2003; Joyce et al., 2007; Wotton and Warren, 2007). Other organisms produce biological material that integrates with surrounding sediments, increasing sediment cohesion. For example, mussels can increase the boundary shear stress required to initiate transport of unconsolidated sediments by facilitating particle adhesion through their excretion of biodeposits and their associated extracellular polymeric substances (Paterson, 1997; Black et al., 2002).

Additionally, many aquatic insects spin silk and use that silk to bind sediment particles, which can make sediments more resistant to entrainment. For example, some caddisflies spin silk nets that they use to capture suspended food particles and attach the base of these nets to streambed gravels, which can strongly influence sediment transport dynamics (Johnson et al., 2009). In a mechanistic model Albertson et al. (2014) showed that these nets can increase the critical shear stress required to initiate sediment motion by 40–70%, while Cardinale et al. (2004) used results from a flume experiment to project that net-spinning caddisflies can increase the recurrence interval of a bed-scouring flood by ~30%. Additionally, other types of caddisflies construct cases out of silk and gravels (in which they reside), which has a similar effect of consolidating smaller sediments into a larger matrix that requires more force to move (Statzner et al., 2005).

4.4.2. Behavior

Perhaps the most profound effects of animals on geomorphological processes is a product of the physical disruption of bed sediments due to varying animal behaviors: moving between the riparian zone and streams (e.g., hippopotami; McCarthy et al., 1998), nest-building, burrowing, and/or feeding. When fish spawn in rivers they often build nests (redds) made of gravels where eggs are laid and fertilized. Some fish, such as salmon, spawn in such large numbers that this nest building can have dramatic impacts on sediment dynamics in rivers. Redd construction can dramatically impact streambed topography and increase local bed surface roughness (Hassan et al., 2015) and can also be extremely disruptive to sediments (Kondolf and Wolman, 1993; Gottesfeld et al., 2004). Schools of spawning salmon can increase the removal and suspension of fine sediments fivefold (Moore et al., 2004) and can initiate the sediment movement at scales greater than floods (Gottesfeld et al., 2004; Hassan et al., 2008).

Large benthic dwelling invertebrates, such as crayfish, are capable of influencing sediment cohesion because of movements and burrowing, sometimes referred to as *bioturbation*. Statzner et al. (2000) found that crayfish movements on top of the streambed (i.e., walking and tail flips) had effects at the scale of entire riffle-pool sequences in artificial stream channels, increasing sediment transport by 140–228%; work that has been supported by other laboratory studies showing effects of similar magnitude (Johnson et al., 2010; Johnson et al., 2011). In addition to increasing the transport of bed sediments, crayfish can also increase the transport of bank sediments by creating burrows in bank sediments, which destabilize them and lead to bank failures during high flow events, changing channel morphology (Harvey et al., 2011). Other relatively large benthic invertebrates also actively burrow in bed sediments, such as freshwater mussels (Fig. 3D; Allen and Vaughn, 2009, 2011). Mussel burrowing behaviors increase water content in sediments (De Deckere et al., 2001; Vaughn and Hakenkamp, 2001; Thrush et al., 2006), resulting in increased sediment erosion facilitated by reduced bulk densities or reduced sediment cohesion (Allen and Vaughn, 2011; Johnson et al., 2011).

Sediment transport dynamics in streams can be strongly affected by animals that forage in the benthos. Many fish are benthic feeders and actively ingest fine sediments, preventing fine sediment accrual during low-flow periods (Power, 1990; Flecker, 1996, 1997). Crayfish can also ingest sediments while feeding, preventing sediment accumulation (Creed and Reed, 2004; Helms and Creed, 2005). Moreover, some benthic feeding fish physically disrupt sediments while searching for prey items, reducing the critical shear stress required to initiate sediment motion by ~60% (Statzner et al., 2003; Statzner and Sagnes, 2008).

4.4.3. Biogeochemical cycling

The role of animals in modulating nutrient cycling has been accepted as an essential component influencing community structure and ecosystem function in aquatic systems (Sterner, 1986; Vanni, 2002; Vanni and McIntyre, 2016; Atkinson et al., 2017). Animals have an important role in biogeochemical cycles because they alter producer and microbial biomass, primary and secondary production, decomposition rates, and nutrient fluxes through direct and indirect effects (Table 1). Animals also directly influence biogeochemical cycling through feeding and excretion of soluble nutrients. Furthermore, they indirectly influence biogeochemical cycling by modifying the physical habitat through sedimentation (i.e. depositing materials on the stream bottom) or bioturbation, or the suspension or movement of sediments through physical activities of the organism (e.g., burrowing, crawling, etc.; Berke, 2010).

The direct effects of animals, such as feeding and excretion, on nutrient regeneration and retention have received a great deal of attention from researchers (Vanni and Layne, 1997; Vanni, 2002; McIntyre et al., 2008; Atkinson et al., 2013; Griffiths and Hill, 2014). Through selective ingestion and assimilation, animals can redistribute nutrients and materials through excretion and deposition egesta, thus influencing particulate materials and nutrient availability and limitation (Flecker et al., 2002; Small et al., 2009; Atkinson et al., 2013; Capps and Flecker, 2013). The specific behavioral and stoichiometric traits of the animals can play an important role as to when and where these effects influence nutrient uptake and propagate up the food web. For example, the stoichiometric traits of a fish, *Astyanax aeneus* (Banded tetra), led to phosphorus being excreted at disproportionately high rates relative to other species in the system and thus supplied ~90% of phosphorus demand to the stream, while nitrogen excretion was not variable across species (Small et al., 2011). Organism movement, such as the daily movements by hippopotami, between the riparian zone and the stream transports large quantities of nutrients (C and N) into the stream through deposition of feces (Subalusky et al., 2015). Behaviors such as aggregating behaviors can also lead to the creation of biogeochemical hotspots and hot moments. McIntyre et al. (2008) showed that aggregations of fish led to biogeochemical hotspots and that their excretion could meet >75% of ecosystem N demand. Furthermore, Atkinson et al. (2013) showed that dense, multispecies aggregations of filter-feeding unionid mussels altered the nutrient limitation status of stream reaches and the benthic algal species composition inhabiting those reaches during base-flow conditions. A study in the same system demonstrated that the biological activities of mussels increased the abundance of biofilm (which can influence sediment transport and biogeochemical cycling; see Algae and biofilms Section above) and invertebrate communities (Spooner and Vaughn, 2006), which only hints at the interactive effects of the entire community on geomorphic and biogeochemical processes.

As discussed above, bioturbation by animals (Vaughn and Hakenkamp, 2001; Holtgrieve and Schindler, 2011; Needham et al., 2011) influences sediment transport (Statzner et al., 2000, 2003; Statzner and Sagnes, 2008) and sediment accumulation (Helms and Creed, 2005). The physical processes of bioturbation, however, also indirectly influence important biogeochemical processes at the benthic-water interface. These indirect effects to biogeochemical cycling can be just as influential as direct regeneration of nutrients by animals, altering nutrient and energy pathways. For example, nitrification ($NH_4^+ \rightarrow NO_3^-$) and denitrification ($NO_3^- \rightarrow N_2(g)$) are nitrogen cycle processes that occur at or below the benthic-water interface. Denitrification is an important process to study as it occurs under anoxic conditions and represents the removal of nitrogen from aquatic ecosystems. Nogaro and Burgin (2014) investigated the effect of a burrowing tubificid in a freshwater mesocosms and found that denitrification was stimulated under higher densities of fauna and higher water column nitrate (NO_3^-) concentration. Marine and invasive freshwater bivalves promote microbial denitrification by influencing the primary drivers of denitrification: enhancing NO_3^- availability, organic carbon quantity and quality, and promoting favorable redox conditions (Newell et al., 2002; Bruesewitz et al., 2006, 2009; Kellogg et al., 2013). In freshwaters, invasive freshwater mussels (i.e., zebra mussels [*Dreissena polymorpha*] and Asian clams [*Corbicula fluminea*]) alter stream sediment denitrification rates, specifically through the direct increase of nitrification and indirectly denitrification through mussel excretion (Bruesewitz et al., 2006; Bruesewitz et al., 2008; Turek and Hoellein, 2015). Bioturbation by Pacific salmon (*Oncorhynchus* spp.) also reduces gross primary production and enhancing heterotrophic processing through redistributing energy and nutrients (Holtgrieve and Schindler, 2011). The inclusion of species traits such as these into an ecogeomorphic framework will help move the science forward and enhance our understanding of the interactive effects of animal communities on geomorphic and biogeochemical processes.

5. Moving the ecogeomorphic framework forward

Many conceptual frameworks have provided foundations for investigating how hydrologic and geomorphic processes influence the structure and function of riverine ecosystems (Vannote et al., 1980; Stanford and Ward, 1993; Tockner et al., 2000; Poole, 2002; Benda et al., 2004; Thorp et al., 2006). Recently, frameworks have been developed that provide a new perspective by including biological feedbacks, presenting ecogeomorphic frameworks where fluvial landforms are bidirectional systems wherein hydrologic and geomorphic processes interact (Riggsbee et al., 2013; Allen et al., 2014; Fei et al., 2014; Julian et al., 2016). Here we broaden these efforts to extend the ecogeomorphic framework to include biogeochemistry and primary production as unifying features of top-down and bottom-up perspectives on fluvial system form and function (Fig. 2).

5.1. Ecogeomorphology: temporal and spatial windows

We suggest that hydro/geomorphological and ecological processes operate on different spatiotemporal scales, generating bidirectional feedback loops over space and time (Fig. 4). As an ecological disturbance, high flows rework riverbeds and floodplains generating habitat heterogeneity, washing out some existing organisms, while transporting nutrients and organic matter received from the watershed (Ward and Tockner, 2001; Ward et al., 2002; Allan, 2004; Doyle et al., 2005). This partially or totally resets the ecosystem and configures the abiotic template for biological activity occurring during base-flow conditions. As ecosystems recover from perturbations and reform as hydrologic and geomorphic processes senesce, a biologically active phase initiates (Fisher et al., 1982; Grimm and Fisher, 1989). Ecosystems process and recycle nutrients brought in from the watershed from runoff during the previous high flow event, using those nutrients to stimulate new growth via primary production (Junk et al., 1989; Murdock et al., 2011). This increase in primary production reverberates throughout the ecosystem, fueling population growth of animals (aquatic insects, fish, etc.) that influence local sediment characteristics (including particle size distributions, sorting, and cohesion) during base-flow conditions and create positive biogeochemical feedbacks that stimulate more primary production (Lohrer et al., 2004; Atkinson et al., 2014b). These biogeomorphic feedbacks can be extended to existing riverine frameworks (e.g., River Continuum Concept, Flood Pulse, Functional Process Zones) to link the geomorphological structure and biology of stream networks interacting with ecological function over temporal and spatial windows.

Primary producers (aquatic macrophytes or biofilms in streams, or riparian trees as floodwaters recede) also influence the hydrologic and/or geomorphologic template, as the biomass produced can serve to physically reinforce instream or streambank sediments or to modify near-bed or near-bank flow patterns during the next high flow event (Wynn and Mostaghimi, 2006; Hopkinson and Wynn, 2009; Pollen-Bankhead and Simon, 2010). Thus, hydro- and geomorphologic processes, operating episodically during bankfull conditions, govern the ecological activity that occurs over longer time periods during base-flow conditions, generating the antecedent conditions that influence the hydro- and geomorphologic processes occurring during the next high flow event. Finally, this bidirectional relationship should

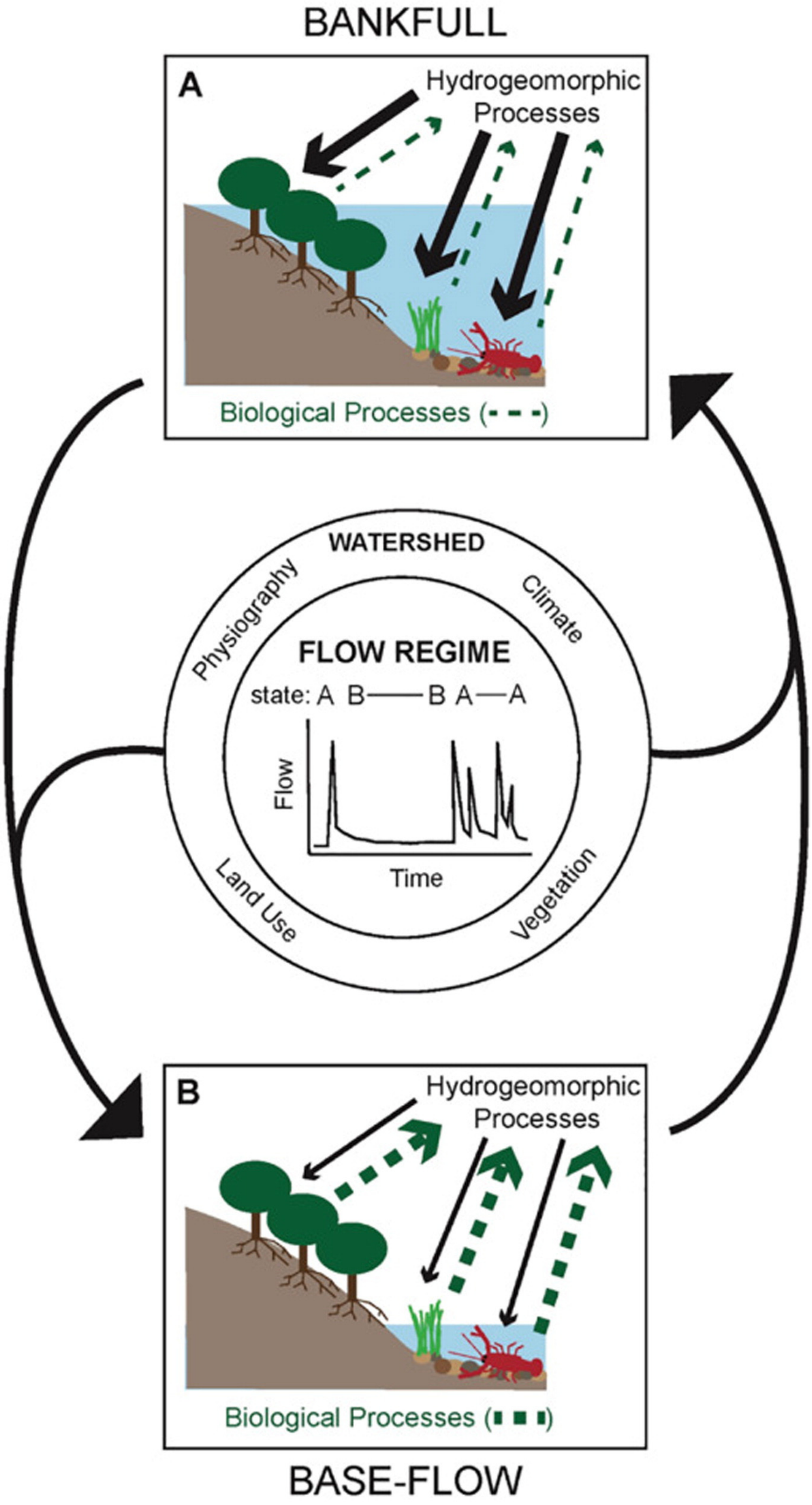

Fig. 4. Conceptual model highlighting the bidirectional feedbacks that are contingent on flow regime. The importance of the biological processes on river geomorphology and biogeochemistry vary considerably as a function of a river's flood frequency and magnitude characteristics. Environmental characteristics (e.g., climate, hydrology) will also likely have a considerable effect on the importance/magnitude of these interactions. During bankfull conditions, (A) hydrogeomorphic processes strongly influence sediment transport and biological processes. For example, a frequently flooded reach will likely be less affected by biological processes. During base-flow conditions (B), however, the system can reset and biological structures can lead to changes in channel form and strongly control biogeochemical transformations.

enhance the resiliency of fluvial landforms, as physical and biological processes pull and push against each other repeatedly over time. This feedback results in biogeochemical activity that represents a function that incorporates the physical and biological template.

The previously discussed case studies lend support to our proposed amendment of ecogeomorphic frameworks to include cumulative species effects on geomorphology and to be more explicitly inclusive of biogeochemical cycles, as they outline the role the stream network plays in determining species distributions (e.g., River Continuum Concept), but also the role species play in ecosystem processes and feedbacks to the geomorphic structure of the system. Disturbance by floods, for example, can greatly alter channel structure and community structure and changing successional dynamics, thus altering biogeochemical cycling. Biological entities, however, can also mediate the influence of such disturbance events; making the inclusion of these feedbacks necessary for making predictions regarding the functioning of river ecosystems. This complexity makes studying these interactions and feedbacks challenging.

The timescales that geomorphologic and ecological processes operate on have implications for riparian and floodplain ecosystems as well. The importance of how these geomorphologic and ecological timescales interact is often made most apparent when they become artificially decoupled. As an example, in many rivers natural disturbance regimes are highly altered by flow regulation and impoundments, such that large floods occur even more rarely than they used to, which has implications for how they interact with ecological processes. Dixon et al. (2015) documented the effects of a 500-year flood in the Missouri River at riparian floodplain forest sites in South Dakota, Nebraska, and Iowa, USA. They found post-flood declines in tree density, particularly in young forest stands. While such declines are to be expected under large floods, under natural conditions they would be offset by increased recruitment post-flood. Dixon et al. (2015) observed widespread cottonwood tree recruitment post-flood, but nearly all seedling patches occurred on sandbars in the active channel rather than on overbank sites, which led to high seedling mortality in the following years. Decades of flow management on the Missouri River reduced the frequency of overbank floods, such that floods merely rework the active channel rather than leading to channel realignment, lateral migration, or avulsive events that create off-channel forest recruitment sites (Stella et al., 2011; Dixon et al., 2015). Thus, although the life-history timelines of cottonwood recruitment and death have not changed, the frequency of overbank flows has decreased. This temporal decoupling limits the restorative effects that large infrequent disturbances would otherwise have naturally and will limit future forest recovery and growth in this system (Dixon et al., 2015).

Changes in riparian zone ecological processes can also influence geomorphological processes, and classic examples here include how the establishment and spread of nonnative riparian plants can lead to changes in river channel geomorphology (Julian et al., 2016). In some cases, these feedbacks can operate under different temporal trajectories even within the same system. The nonnative salt-cedar (*Tamarix* spp.) has spread widely throughout riparian zones across the western USA. In a study of the Yampa River in Colorado, a river that was previously largely devoid of dense vegetation in the channel, Manners et al. (2014) observed that salt-cedar establishment into mid-channel bars was incremental over the first three decades of its establishment. Likewise, its effects on channel morphology were incremental, as the salt-cedar plants now present mid-channel the induced sediment deposition and led to an incremental vertical accretion of the bars they inhabited. But once bars accreted above the elevation of the mean annual flood, salt-cedar establishment and its associated effects on channel change rates increased substantially, leading to a rapid, coupled, ecological, and geomorphological change (Manners et al., 2014).

Few ecogeomorphic studies have investigated interactions among species (but see, Gerbersdorf et al., 2008; Allen and Vaughn, 2011; Albertson et al., 2014) even though these systems contain species-rich communities that interact. Freshwater ecosystems have experienced the greatest loss of biodiversity in comparison to terrestrial and marine systems, thus it is pertinent to determine the role interacting communities play in affecting geomorphic and biogeochemical processes. We suggest using the species traits of the organisms themselves as well as the habitats in which they reside. The traits may include attributes, such as autotroph vs. heterotroph, taxonomic affiliation, feeding guild, body size, and habitat preference. Considerable interest exists for ascertaining the roles of species identity and biodiversity in mediating ecosystem processes (Loreau et al., 2001; Vaughn, 2010). Thus, the exploration of variation among freshwater organisms and the feedback between the geomorphic template and the resulting impact on nutrient cycling may offer an excellent means of addressing how the abiotic template and the communities and succession of organisms interact to influence essential ecosystem functions.

Biogeochemical nutrient cycles represent the conversations that occur as a result of interactions between geomorphological and biological systems. As such, a more explicit inclusion of the biogeochemical template is essential for moving river research forward. In the case of a disturbance, abiotic processes (i.e., abrupt changes in hydrology and geomorphology) can dominate stream biogeochemistry. Given sufficient time between disturbances, the influence of biotic processes (i.e., primary production, filter feeding, sediment/nutrient retention by riparian vegetation) can also dominate stream biogeochemistry. Reflecting on the case studies, the influence of a single organism on stream biogeochemical cycles may be minute, but populations of organisms performing a specific ecosystem function over time can have large effects on stream biogeochemistry, which in turn feeds back to the geomorphology of a stream. Future research could explore the relative influences of the biotic and abiotic environment on biogeochemical cycles on multiple scales, be it spatial, temporal, or across situations such as natural or anthropogenic disturbance events. The dynamic relationship between stream geomorphology and biodiversity creates biogeochemical feedbacks (e.g., consumption and nutrient cycling) that improve the resiliency of a lotic system. Viewing an organism as though it were a potential geomorphic control on an ecosystem could elucidate new insights from a bottom-up (time-integrated) perspective of the organism's importance on overall ecosystem function and resiliency.

5.2. Perspectives, tools, and methods going forward

The case studies previously summarized make it clear that many biogeomorphic feedbacks, as well as the direct and indirect processes by which organisms are involved in biogeochemical cycling, occur at the meter scale and are spatially heterogeneous. Ongoing and future research endeavors must be designed to not only capture small-scale measurements of biophysical processes but also apply them to larger geomorphic units (Fig. 5; reach or segment, for example) to identify potential geomorphic engineers and the conditions under which they are influential. Fortunately, fluvial topography can now be mapped at the meter-scale (Gonzalez and Pasternack, 2015) using technology, such as LiDAR (Cavalli et al., 2008; Lallias-Tacon et al., 2014, 2017) and aerial imagery collected using UAVs (unmanned aerial vehicles) in floodplains, riparian zones, and even in-channel measurements of shallow or dry rivers. Alternatively, side-scan sonar can be used in wet and turbid river systems (Goclowski et al., 2013; Smit and Kaeser, 2016). The proliferation of riverbed digital elevation maps generated by these new technologies motivated Gonzalez and Pasternack (2015) to differentiate spatially explicit, process-based, comprehensive data concerning fluvial landforms as near-census river science. Census data collection should become a reality with future technological advancements that permit a finer-level (<1 m spatial resolution) of bed topography data to be captured (Kammel et al., 2016).

Near-census river science is already making progress toward explaining and predicting spatial and temporal heterogeneity of habitat and geomorphology based on measurements of biophysical processes

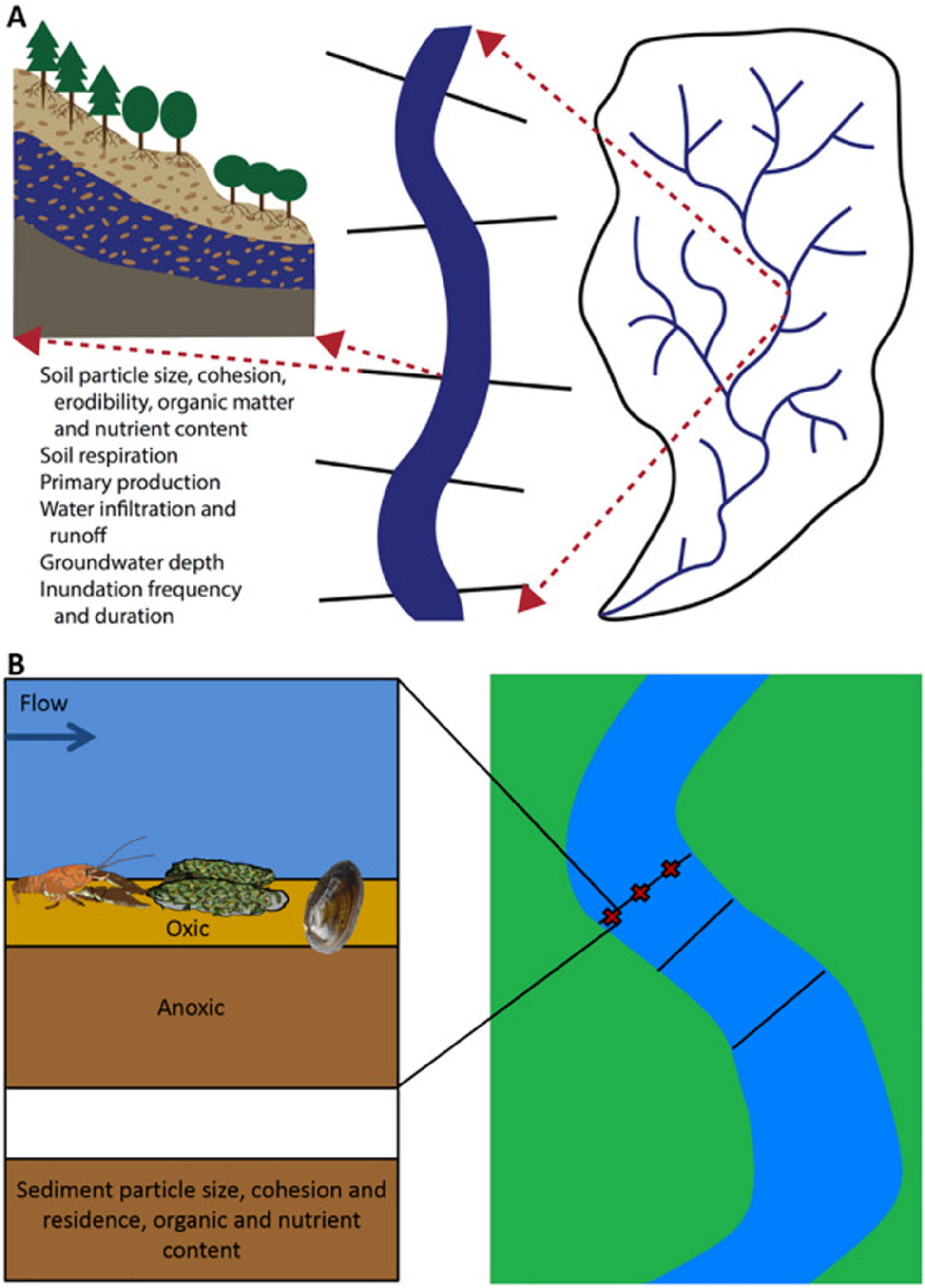

Fig. 5. We propose incorporating a field-based approach to better understand the feedbacks between the abiotic and biotic components of the stream and their impacts on ecosystem function. This conceptual diagram highlights a potential sampling scheme in which at (A) the watershed-scale specific reaches can be selected, and fine-scale processes of riparian species composition and their effects on fluvial and ecosystem processes can be measured. Further, (B) large-scale (stream panel) stream morphology (bankfull width, channel width, depth) can be paired with more fine-scale measurements made at the patch scale within the stream. We propose that organism abundances or densities should be quantified at the patch scale along with sediment characteristics (e.g., sediment particle size, organic and/or nutrient content). These patch-scale measurements can also include measurements of the riparian community in relation to sediment and reach-scale (e.g., bed movement) characteristics as in (A). Collectively, these measurements within the riparian area and in the stream can be paired to measurements of ecosystem function such as sediment denitrification and nitrification, reach nutrient uptake, and/or ecosystem metabolism.

occurring at small spatial scales (Fig. 5). Digital elevation maps of floodplains and river channels made from new technologies are used to map geomorphic complexity, such as spatial variability of sediment facies (Kammel et al., 2016), and to measure net erosion and deposition for a reach or segment over years (Wheaton et al., 2010a, 2010b). Digital elevation maps can be paired with small-scale measurements of biophysical processes and 2D/3D hydrodynamic models to create large-scale (reach, segment, or floodplain) maps of aquatic habitat based on species level needs and geomorphic variability (sediment particle size, channel morphology mapping, for example) (Bonetti et al., 2016; Kammel et al., 2016). Recent advances made in virtual geographic environment models (Zhang et al., 2016) permit multiple models from different disciplinary perspectives to interact and discern changes in processes over complex spatiotemporal arrangements, opening the door to ecohydrogeomorphic synthetic studies. Synthetic studies permit the use of highly experimental frameworks that can be designed to identify potential new relationships and controlling mechanisms, to direct new avenues of field and lab research, and to address complex questions concerning spatial and temporal scaling issues that are not practical to test in physical environments because of their scope. Lin et al. (2016) used such an approach to examine whether the spatial configuration of geomorphic habitat units could potentially alter the net denitrification of a 2.5-km study reach based on model input data from an actual river, as a consequence of water residency time within different geomorphic habitat units. Lin et al. (2016) showed that geomorphic unit configurations with pools occurring first yielded the most potential for denitrification, with all other conditions being equal. Kammel et al. (2016) make a strong case that whenever models are used to predict or map habitat conditions two forms of model validation should take place: (i) validation of the model's ability to represent hydrodynamic conditions, which they equate to the generic and engineering-based form of model validation; and (ii) bioverification, which seeks to confirm the model's ability to represent physical habitat based on observed biological uses of the environment.

Essential to the integration of small-scale biophysical measurements and spatially explicit data sets derived from digital elevation maps and 2D/3D hydrodynamic models are: (i) experimentally based measurements, particularly field-based ones; and (ii) higher standards for model validation processes. The vast majority of direct measurements of organism alteration of sediments, for example, come from laboratory or flume-based studies (see excellent review by Grabowski et al., 2011). More direct measurement of bioeffects on rivers is needed from field settings where organisms are acting as members of communities and where the complexity of physical environments can be more accurately represented. Several researchers use manipulations as part of their research design to achieve direct measurements in field settings. Rex et al. (2014) established outdoor flumes to examine bed material and nutrient enhancement of rivers by Pacific salmon, for example. In some instances it may be productive to pair lab-based experiments with field-based measurements, as Harvey et al. (2014) did with mesocosm experiments and field measurements to determine the effect of crayfish on sediment yields.

Previous ecogeomorphic frameworks suggests that hydrologic and geomorphic data be collected on smaller scales. In moving forward with the proposed framework, we contrarily suggest studies of the biotic influence on geomorphology, hydrology, and biogeochemical cycles be conducted across multiple spatial scales, such that studies conducted at smaller scales can be upscaled to reveal larger-scale patterns. Examining the distribution and community structure of stream ecosystem engineers at the reach and watershed scales will provide insights to their influence on overall ecogeomorphology of a stream. In lotic and fluvial ecosystem research, there is increasing interest in the transport of materials ranging from nutrients, pollutants, particulates, and sediment in streams and floodplains. The case studies in this article present examples in which organisms and biological communities either help or hinder the transport of dissolved and particulate matter. In fluvial environments, local influences are not always confined spatially. Therefore, understanding the influence of ecosystem engineers across spatial and temporal scales is essential to understanding freshwater and riparian biota in an ecogeomorphic context. Also, with increasing interest in the context-dependency of ecosystem services, collaborations spanning across multiple watersheds, regions, biomes, etc. will be necessary to infer the large-scale ecogeomorphic influence of an ecosystem engineer. One possible approach is *hyperscaling*, where fine-scale data is collected across broad spatial scales, allowing for upscaling of fine-scale data with basins and multiscalar comparisons within and between basins (Fonstad and Marcus, 2010). Such collaborations exist in ecological research (see Mulholland et al., 2001, 2008; Needham et al., 2011; Rüegg et al., 2016), yet current research fails to address interactions and feedbacks between the biotic and abiotic environments that makeup the ecogeomorphic framework.

6. Conclusions

Ultimately, abiotic conditions control the distributions of organisms, yet living and dead organisms have the potential to alter sediment flux and compaction that may have important implications for ecosystems processes. Feedbacks between geomorphic and ecological components are developmentally intertwined. These biophysical interactions are essential to improving predictions of sediment and nutrient yields and biogeochemical cycling in rivers. The lack of biophysical integration within existing ecogeomorphic frameworks impose substantial limitations on their usefulness in understanding and predicting fluvial and biogeochemical changes in the face of projected land use and climate change. Biogeochemical cycles are influenced heavily by physical process; but nutrient transformations are often mediated by biological activity, and the biological cycling of nutrients has implications for fostering ecosystem biodiversity, leading to increased resiliency. While the physical template of many systems has been changed (Julian et al., 2016), so have the biological communities that inhabit these systems. Freshwater diversity has declined at an alarming rate, having substantial impacts on the structure and functions of ecosystems (Dudgeon et al., 2006; Strayer and Dudgeon, 2010; Vaughn, 2010; Allen et al., 2012). Thus, to better understand the resiliency of these systems we need to incorporate species interactions, species diversity, and trait diversity to understand physical (Allen et al., 2014; Albertson and Allen, 2015) and biogeochemical (Spooner and Vaughn, 2008; Atkinson et al., 2014a) processes. Further work along this research vein will permit insights for understanding how rivers and ecological systems codevelop. We hope that future work will examine the bidirectional feedbacks over temporal and spatial scales between the physical and biological systems and the resulting impacts on ecosystem processes.

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