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PRIMER

Ecosystem engineers in rivers: An introduction to how and where organisms create positive biogeomorphic feedbacks

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Ecosystem engineers substantially alter physical flow characteristics and shape a river's form and function. Because the recurrence interval of geomorphic processes and disturbances in rivers commonly match the temporal scale of plants' life cycles or alterations by animals, the resulting feedbacks are an important component of rivers. In this review, we focus on biota that directly or indirectly induce a physical change in rivers and cause positive feedbacks on the functioning of that organism. We provide an overview of how various ecosystem engineers affect rivers at different temporal and spatial scales and plot them on a conceptual gradient of river types. Various plants engineer the river environment through stabilizing sediment and reducing flow velocities, including macrophytes, woody plants, and algal mats and biofilms. Among animals that engineer, beaver that build dams cause substantial changes to river dynamics. In addition, benthic macroinvertebrates and mussels can stabilize sediment and reduce velocities, and aquatic and riparian grazers modulate the effect of plants. Humans are also considered river ecosystem engineers. Most of the ecosystem engineers reported in literature occur in rivers with low to intermediate relative stability, intermediate channel widths, and small to intermediate grain sizes. Ecosystem engineers that create positive biogeomorphic feedbacks are important to take into account when managing river systems, as many common invasive species are successful due to their engineering capabilities. River restoration can use ecosystem engineers to spur holistic recovery. Future research points towards examining ecosystem engineers on longer spatial and temporal scales and understanding the co-evolution of organisms and landforms through engineering.

This article is categorized under:
Water and Life > Nature of Freshwater Ecosystems
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1 | INTRODUCTION

A river's form and function can be described as the balance between the energy of the water and the amount and size of sediment. Across river systems, however, engineering organisms can substantially alter the physical flow characteristics, with broad implications on riparian and aquatic ecosystem functioning. Although examples of aquatic ecosystem engineers have been discussed since the early 1900s (Ruedemann & Schoonmaker, 1938) and terrestrial engineers were even discussed by Darwin (1881), the concept was not defined until the mid-1990s. Originally, the term "keystone species" (Mills, Soule, & Doak, 1993; Paine, 1969) was coined to describe a species that has a disproportionately large impact on its environment relative to its abundance. The classic example is that of a large predator that controls prey populations. The concept of "niche construction" is slightly closer to that of ecosystem engineering, where organisms create their own niche, which most often

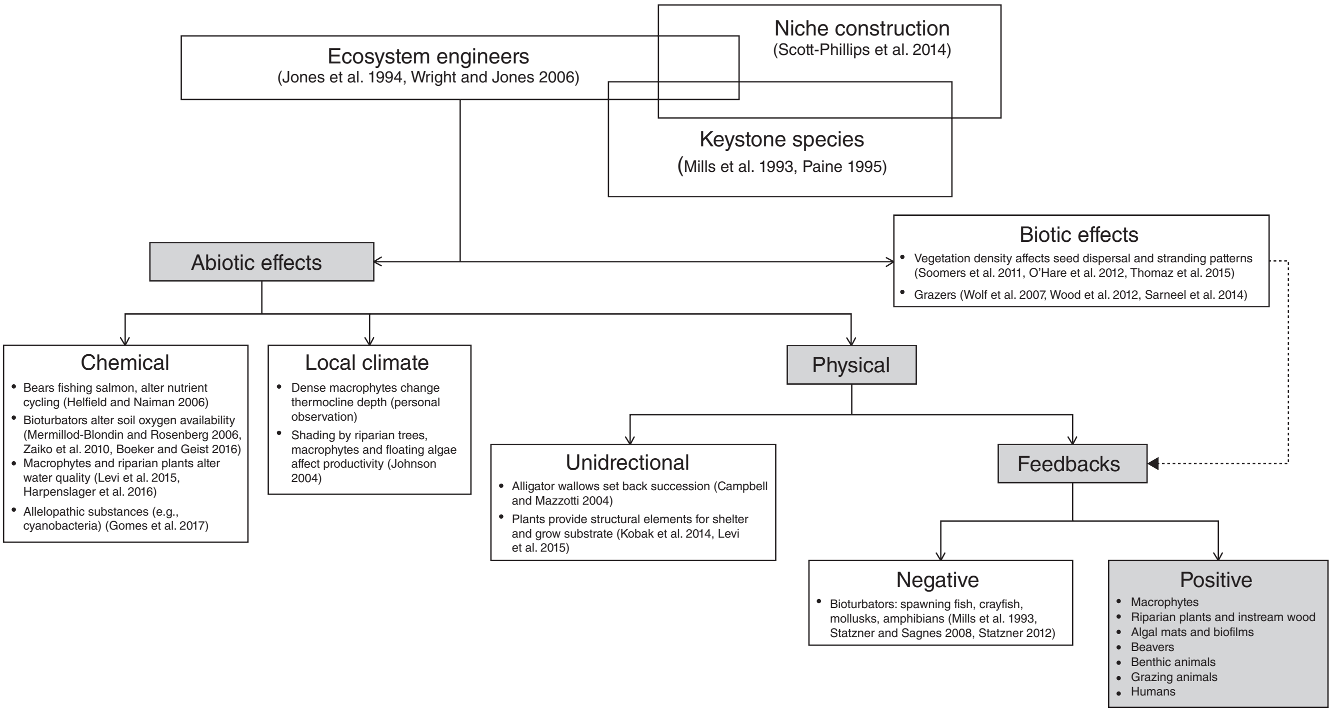

FIGURE 1 Schematic overview of different ecosystem engineers in river systems, categorized according to their engineering effect. Gray shading indicates the type of ecosystem engineers described in this review. The position of the "ecosystem engineers," "niche construction," and "keystone species" concepts are only meant to show that there is overlap and not the degree to which the concepts overlap. A full reference list is provided in Appendix S1, Supporting information. References for ecosystem engineers with positive feedbacks can be found in the text

involves modification of the environment (Figure 1; Odling-Smee, Laland, & Feldman, 2003; Scott-Phillips, Laland, Shuker, Dickins, & West, 2014). The term "ecosystem engineer" overlaps partly with these concepts, defined as "organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain, and/or create habitats" (Jones, Lawton, & Shachak, 1994). Jones et al. (1994) distinguished between autogenic engineers, which create habitat through their own growth, by their own living or nonliving tissue, and allogenic engineers, which transform living or nonliving materials from one physical state to another, via mechanical or other means, thus creating a structure that is left behind. In rivers, autogenic engineers may be something as simple as a large tree that forms an obstacle in the flow, whereas allogenic engineers, such as beaver, transforms trees to dams, creating ponds and extending riparian habitats. Beavers were recognized as "agents of biogeomorphic change" (Butler, 1991; Ruedemann & Schoonmaker, 1938) and "keystone species" (Naiman, Johnston, & Kelley, 1988) long before the introduction of the concept of ecosystem engineers. They are still the flagship species of freshwater ecosystem engineers (Gurnell, 1998; Gurney & Lawton, 1996; Jones et al., 1994), and 20% of the 301 Web of Science hits containing "ecosystem engineer*" refined with "stream or river," deal with beavers.

Because the recurrence interval of geomorphic processes and thus disturbances in rivers (e.g., flooding, shear stress, erosion and deposition) commonly match the temporal scale of plants' life cycles or mechanical alterations by animals, the resulting feedbacks are an important component of river systems. Therefore, in this review we focus on biota that directly or indirectly induce a physical change in rivers that cause positive feedbacks on the functioning of the organism. We prefer this more strict definition than that given by Jones et al. (1994), because these types of ecosystem engineers, which encompass both autogenic and allogenic engineers, directly shape both a river's form and function and positively affects the individual organism or species. Given the strong importance of the river form and function, this can have long-term and large-scale effects on the ecosystem functioning, which can be both positive and negative (Gurnell, 2014; van de Koppel, Herman, Thoolen, & Heip, 2001). Other organisms that engineer the chemical, climatic, biotic, or physical environment without biogeomorphic feedbacks are summarized in Figure 1. In this review, we describe where known examples of freshwater ecosystem engineers occur within river systems, in terms of river types and three geomorphic characteristics (relative stability, channel width, and grain size) that control the potential of ecosystem engineers to create positive biogeomorphic feedbacks in rivers. Finally, we summarize the current knowledge of the role of ecosystem engineers in river management and restoration, including invasive species management.

2 | ECOSYSTEM ENGINEERS THROUGHOUT THE RIVER SYSTEM

Instream and riparian ecosystem engineers can be found throughout a river system, from the headwaters to the mouth, in gravel-bed or sand-bed channels, and in dynamic braided systems or stable channels with cohesive or very coarse sediment. The dynamics of the river system will set boundaries for an ecosystem engineer's survival. Within those boundaries, the organism will only engineer and cause positive biogeomorphic feedbacks where resources are available (Moore, 2006), such as fine sediment to be trapped or stabilized. In more general terms, their ecosystem engineering capacity is considered to be context-dependent (Jones et al., 2010; Wright & Gribben, 2017). In a recent meta-analysis, animal ecosystem engineers have indeed been found to have larger effects in rivers with low discharges or hydrologic energy and with small sediment sizes (Albertson & Allen, 2015; Moore, 2006). In addition to physical constraints, the behavior, body size, and population density of the engineering organism influence the impact it will have on its environment (Moore, 2006). In general, it is hypothesized that at intermediate disturbance and sediment supply levels, ecosystem engineers will profit most from their physical impacts (Gurnell, 2014; Wright, Jones, & Flecker, 2002). In order to provide an overview of this hypothesis, we plotted the range of where different organisms actively engineer and create positive biogeomorphic feedbacks based on three process- and form-based geomorphic characteristics of rivers: relative stability, channel width, and sediment grain size (Figure 2). These characteristics were chosen based on many previous river channel classifications that incorporate sediment size and channel stability (Schumm, 1977); however, previous classifications lack a distinction between channel sizes, a critical factor in ecological river characterization such as the river continuum concept (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). Channel size plays a central role in determining how much a certain ecosystem engineer can affect its environment (e.g., a log jam in a wide channel will not affect flow as much as a log jam in a narrow channel). Stream power and slope determine the potential of ecosystem engineers to survive and be able to alter hydrodynamics; these factors are incorporated within the "relative stability" factor that relates to both lateral stability and bed disturbances (i.e., bedload transport); in rivers with high relative stability, resisting forces (e.g., sediment size, cohesivity, and yield) exceed driving forces (e.g., stream power, shear stress). We plotted the domains where different ecosystem engineers are reported to be both active and able to create positive feedbacks (Figure 2).

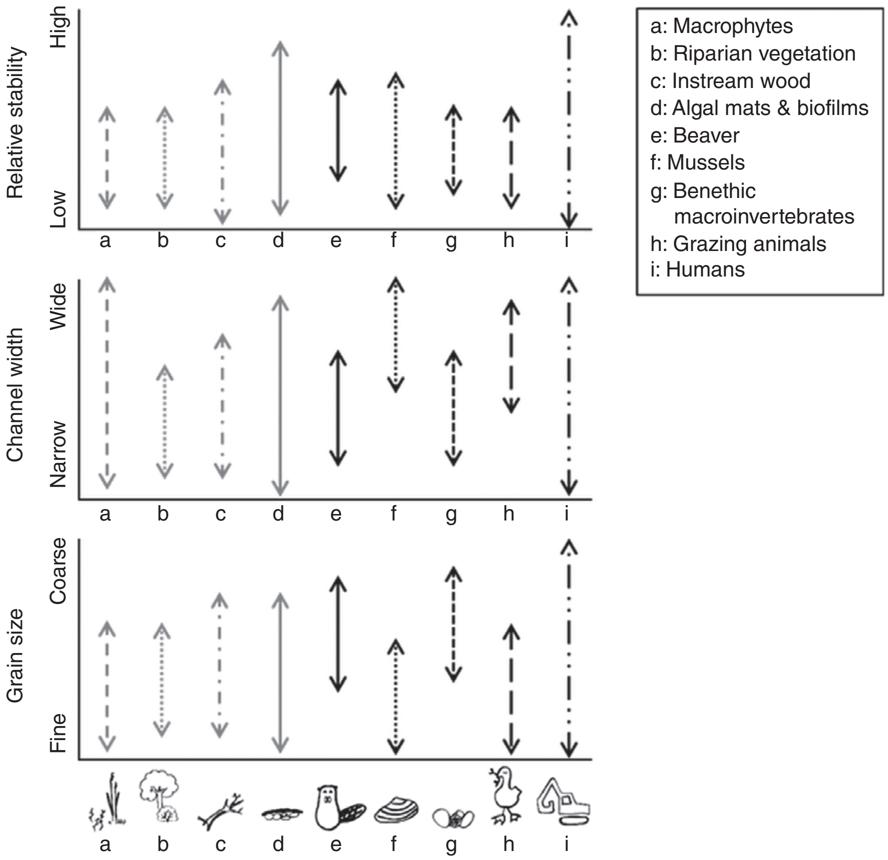

FIGURE 2 Diagrams denoting where different ecosystem engineers actively engineer the environment and create positive biogeomorphic feedbacks in rivers based on three process- and form-based geomorphic factors: relative stability, channel width, and grain size. Note that these organisms may be present in other parts of the river system but may not act as ecosystem engineers there (e.g., beaver occur in wide channels with fine sediment, but they do not build dams there), and that the ecosystem engineering capacity may be context dependent within the approximate space shown in the diagrams, depending on other, nongeomorphic environmental factors (e.g., temperature, nutrient availability)

3 | EXAMPLES OF ECOSYSTEM ENGINEERS IN RIVERS

3.1 | Plants

3.1.1 | Macrophytes

Submerged macrophytes are usually very flexible, allowing them to adjust to the changes in hydraulic properties and to hide in the laminar sub-layer or boundary layer of the channel bed (Bornette & Puijalon, 2011; Puijalon et al., 2011; Schoelynck et al., 2013). Emergent macrophytes require stiffer stems as they have to carry their own weight above water, which restricts their occurrence to river margins and less turbulent flows (Figure 2). Almost all macrophytes are clonal and grow in dense, streamlined patches that typically expand in the downstream direction (Barrat-Segretain, Bornette, & Hering-Vilas-Boas, 1998; Bornette & Puijalon, 2011). Within the dense vegetation patches, flow velocity decreases, thus increasing sedimentation (Gurnell, van Oosterhout, de Vlieger, & Goodson, 2006). This effect resulted in a 15-cm bed elevation difference between vegetated and nonvegetated patches in a Belgian lowland river, the Zwarte Nete River (Schoelynck et al., 2013). On larger spatial scales, negative feedbacks may appear; acceleration of the flow next to the patch and high turbulence downstream of the patch (Gurnell et al., 2006; Liu, Diplas, Hodges, & Fairbanks, 2010; Schoelynck et al., 2013; Trinci, Harvey, Henshaw, Bertoldi, & Holker, 2017) can restrict plant growth (Bornette & Puijalon, 2011; Schoelynck et al., 2013). The spacing between the patches can determine the strength of these negative feedbacks (Bal et al., 2011). With their engineering effect on flow velocity, macrophytes can facilitate the colonization of other species, either through higher seed deposition (Gurnell, Thompson, Goodson, & Moggridge, 2008; Soomers et al., 2011) or by providing shelter and structural support for terrestrial species (Azza, Denny, van de Koppel, & Kansiime, 2006). Water level fluctuations (e.g., during flooding) can affect the engineering capacity of macrophytes either by enhancing seedling establishment and vegetation density (Balke, Herman, & Bouma, 2014; Sarneel, Janssen, Rip, Bender, & Bakker, 2014b) or by affecting growth forms, as some macrophytes alter their stem characteristics when exposed to air (e.g., *Berula erecta*, *Persicaria amphibia*; De Wilde, Sebei, Puijalon, & Bornette, 2014).

3.1.2 | Riparian plants and instream wood

Riparian plants occur along most river types, and although they are often not directly exposed to river flows, their location at the banks makes them important autogenic river engineers (Gurnell, 2014). First, they add tensile strength to the bank material, increasing overall bank cohesion, which stabilizes streambanks and reduces the likelihood of bank collapse or mechanical erosion (Abernethy & Rutherfurd, 1998; Pollen-Bankhead, Simon, & Thomas, 2013; Simon & Collison, 2002). Second, the stems and above-ground biomass modify the flow field, when flooded, with similar mechanisms as macrophytes by increasing turbulence and decreasing velocities (Liu et al., 2010; McBride, Hession, Rizzo, & Thompson, 2007). On long temporal scales, the emergence of terrestrial plants during the Paleozoic (~400 Ma) altered channel form from solely braided to anabranching and meandering (Gibling & Davies, 2012). Similarly, flume experiments have shown that vegetation is required to create self-forming multithread meandering channels (Tal & Paola, 2010). Both below-ground and above-ground, the physical engineering capabilities depend on species-specific traits (Bornette & Puijalon, 2011; Gurnell, 2014), for example, trees and shrubs have higher tensile strengths than forbs and graminoids (Polvi & Wohl, 2013).

Together with woody riparian vegetation, instream wood can have engineering effects in small- to medium-sized rivers (including up to relatively large European alluvial rivers, ~500 m in width) with fine- to medium-sized sediment (Figure 2), forming complex, dynamic anabranching channels with vegetated islands (Collins, Montgomery, Fetherston, & Abbe, 2012; Gurnell & Petts, 2002). Rivers that were previously braided retain a multithread character, but become more stable with islands, whereas rivers that were previously single-threaded and meandering become more dynamic, forming a multithreaded planform with vegetated islands. In contrast, in very wide alluvial rivers (e.g., the lower Mississippi River and the Amazon River), accumulated instream wood, known as log jams, likely have a much smaller effect on channel form. Log jams alter flow hydraulics and induce sediment deposition, forming sediment bars; woody riparian vegetation can establish on the bars, transforming the bars into stable islands. When these islands are eroded, more instream wood is recruited, forming new log jams that encourage sediment deposition, and a new floodplain- large wood cycle starts (Collins et al., 2012). Similarly, in mountain streams, if the wood size to channel size ratios exceed a threshold, multithread channels form (Wohl, 2011). Throughout the Holocene, multithread channels were likely very common and widespread (Polvi & Wohl, 2013), but with the (recent) removal of old-growth forests, rivers have lost a key ecosystem engineer.

3.1.3 | Algal mats and biofilms

Algal mats and aggregates of unicellular organisms (biofilms) can have different shapes depending on flow and sediment characteristics (Battin, Kaplan, Newbold, & Hansen, 2003; Besemer et al., 2007; Rusconi, Lecuyer, Guglielmini, & Stone, 2010). River bed sediment covered by biofilms will have a smoother surface and will protect the sediment from erosion.

Although their ecosystem engineering capacity is poorly quantified in freshwater systems (but see Battin et al., 2003), there is marine evidence that aggregation of unicellular organisms can create positive feedbacks and even new stable ecosystem states (van de Koppel et al., 2001).

3.2 | Animals

3.2.1 | Beavers

Beavers alter their environment by gnawing and felling riparian trees (e.g., willows, aspen, alder) for food and building dams, which in turn creates more suitable habitat through upstream ponding and higher water table levels (Gurnell, 1998; Westbrook, Cooper, & Baker, 2006). Beavers are found in nearly all types of rivers in Europe and North America but only build dams in rivers with low channel gradients (<4%), relatively low widths (<10–15 m) without bedrock channel boundaries, and with stable flow regimes (Figure 2). Beaver dams have multiple biogeomorphic effects such as decreasing channel slopes and flow velocities, which increases fine sediment deposition (Butler & Malanson, 1995; Pollock, Beechie, & Jordan, 2007). Through overbank flooding and subsequent channel avulsions, a more complex multithread channel network commonly forms (John & Klein, 2004; Polvi & Wohl, 2012). At the scale of the entire valley bottom, dam-building by beaver creates larger and more complex riparian areas (Green & Westbrook, 2009), which has cascading effects on other fauna that depend on riparian zones (Cooke & Zack, 2008), and increases local and regional biodiversity (Stringer & Gaywood, 2016).

3.2.2 | Benthic animals

Quite a few benthic macroinvertebrates, such as some midges and caddisflies, can spin silk nets between boulders, and are thus allogenic engineers that can create low-velocity environments and increase sediment stability, mostly in rivers with intermediate sediment sizes and with intermediate channel stability (Cardinale, Gelmann, & Palmer, 2004; Nakano, Yamamoto, & Okino, 2005). The nets are used as retreats for larva or as capture nets to strain out food from the flowing water and may decrease local velocities (Nakano et al., 2005). In addition, net-spinning caddisfly larvae also serve to consolidate bed sediment, and have been reported to double the critical shear stress required to entrain and transport sediment, thus decreasing overall bed sediment transport (Albertson, Cardinale, & Sklar, 2014; Johnson, Reid, Rice, & Wood, 2009; Statzner, 2012; Takao, Negishi, Nunokawa, Gomi, & Nakahara, 2006).

Depending on whether mussels are burrowing or sedentary, they can have opposing effects on their physical environment. Sedentary mussels can be considered autogenic ecosystem engineers that enhance their environmental conditions by creating dense, cohesive mussel beds that reduce flow velocities, consolidate sediment, and act as a protective cover from erosion for beds with fine sediment (Allen & Vaughn, 2009), such as in deltas, tidal marshes or in large alluvial meandering and anabranching rivers. Burrowing mussels, on the other hand, have been shown to increase erosion through bioturbation (Allen & Vaughn, 2009).

3.2.3 | Grazing animals

Grazing animals such as waterfowl, muskrat, capybara, snails, and fish, and also a variety of terrestrial animals in the riparian zone, can substantially modify the extent of instream, emergent, and riparian plant cover (Sarneel, Huig, Veen, Rip, & Bakker, 2014a; Wood, Stillman, Clarke, Daunt, & O'Hare, 2012). Through grazing, the vegetation is kept more open and accessible for the grazers, which, for instance, allows them to better escape predators (van den Wyngaert, Wienk, Sollie, Bobbink, & Verhoeven, 2003).

3.2.4 | Humans

Humans are the most influential ecosystem engineer in (almost) every river type (Figure 2). They have built dams and levees and have altered the course of rivers in order to increase the amount of suitable habitat and provide water for drinking and growing crops (Baron et al., 2002; Nilsson, Reidy, Dynesius, & Revenga, 2005). Currently, humans are altering rivers through management and restoration, in order to achieve higher levels of other ecosystem services, including recreation, water purification, and flood risk reduction (Palmer, Filoso, & Fanelli, 2014; Palmer, Menninger, & Bernhardt, 2010; Wang et al., 2016).

3.2.5 | Bioturbators

Bioturbators, which are often considered a type of ecosystem engineer, disturb and cause erosion or transport of bed or bank sediment. However, it is currently still debated whether they directly or indirectly benefit from their physical disturbance, or if they instead experience negative feedbacks. Some studies suggest that feedbacks may occur via oxygen, light or nutrient availability (Meysman, Middelburg, & Heip, 2006) and may even induce biological feedbacks trough seed dispersal or burial (Blackburn & Orth, 2013). Many animals act as bioturbators at varying scales, including alligators, stoneflies, and tadpoles

(Jones et al., 1994; Meysman et al., 2006; Statzner, 2012). For example, salmonids cause bed sediment coarsening and increased bedload transport during nest (redd) building (Hassan et al., 2008; Kondolf, Sale, & Wolman, 1993), creating hummocky surfaces (DeVries, 2012; Hassan et al., 2008). Similarly, crayfish disturb sediment during burrowing, feeding, and while walking or suddenly escaping predators (Statzner, 2012; Statzner, Peltret, & Tomanova, 2003). In crayfish-impacted areas, the critical shear stress required to move sediment can decrease by 75%, resulting in a greater transport of fine sediment (Statzner, 2012).

4 | ECOSYSTEM ENGINEERS IN RIVER MANAGEMENT

Management of river environments involves both the removal of invasive ecosystem engineers (Crooks, 2002) that have had unintended consequences and the encouragement or introduction of ecosystem engineers for holistic restoration. Management via ecosystem engineers may potentially be more effective than separately addressing many individual problems concerning a river's ecological and physical integrity, since ecosystem engineers may push the system as a whole back into its original stable state (Angelini et al., 2016; Pollock et al., 2014), and interactions between the engineers can further stabilize the system (Marshall, Hobbs, & Cooper, 2013).

4.1 | Invasive ecosystem engineers

Ecosystem engineering is one of the most common mechanisms by which invasive plants and animals, that is, those that are not native to an area that are capable of causing harm to native species and the environment (Crooks, 2002), gain dominance (Ehrenfeld, 2010). About 30% of the organisms in the list of "100 of the world's worst invasive alien species" have direct biogeomorphic effects, another 51% have potential indirect effects, whereas only 19% were judged to have no biogeomorphic impacts in a global review (Fei, Phillips, & Shouse, 2014). Invasive plants are numerous in river systems (Hussner et al., 2017), and two plant species are among the top 10 of the most studied invasive species: *Spartina alterniflora* and *Phragmites australis* (Gallardo, Clavero, Sanchez, & Vila, 2016). The connectivity of river systems allows invasive species to spread easily through active migration or passive dispersal of propagules.

Two cases of invasive species in rivers—the riparian shrub tamarix in North America and beaver in South America—are examples of purposeful introduction of a species to serve a certain purpose which has resulted in unintended consequences. The Eurasian woody shrub tamarix, was introduced in the southwestern United States to decrease bank erosion. Tamarix is a stronger engineer than native willow as mature plant (Wilcox & Shafroth, 2013). However, under unregulated peak flows, tamarix seedlings are outcompeted by native willow. Under decreased peak flows, such as below dams, tamarix has competitive advantage. The increased damming together with a good dispersal capacity of tamarix has resulted in an explosive spread and has caused much larger biogeomorphic change than desired (Dean & Schmidt, 2011).

Whereas beaver (*Castor canadensis* and *C. fiber*) were once widespread in North America and Europe, beaver are non-native to South America. They were introduced to southern Patagonia in 1946 for hunting where they have had a multitude of unintended effects such as the facilitation of additional establishment of invasive plants (Westbrook, Cooper, & Anderson, 2017). Beaver currently occupies approximately 90% of the river systems in the Argentine portion of Tierra del Fuego (Lizarralde, 1993) which has caused the largest alteration to forested landscapes since the end of the last ice age, 10,000 years BP (Anderson et al., 2009).

4.2 | Restoration

4.2.1 | Beaver re-introduction

Restoration of river systems can take advantage of the engineering capabilities of certain species in order to holistically restore a river's geomorphic processes and ecosystem. The use of beaver dams or their analogues within their native geographical range can accelerate the recovery of incised streams (Pollock et al., 2014). The introduction of other keystone species can create the conditions necessary for existent beaver to expand. That is, when wolves were re-introduced into Yellowstone National Park in the western United States, elk behavior changed so that they spent less time browsing riparian areas, providing more food and dam-building material for beaver (Marshall et al., 2013). In areas without wolves, elk dominated, which reduced riparian vegetation, destabilizing streambanks, creating wider channels that became unstable and braided (Beschta & Ripple, 2006; Beschta & Ripple, 2008; Wolf, Cooper, & Hobbs, 2007). In contrast, in areas where wolves have been re-introduced, riparian tall willow communities have recovered, stabilizing streambanks and providing food for beaver, stimulating its spread, which further increase riparian zone area and richness.

4.2.2 | Marsh planting and macrophyte establishment

After abiotic conditions are restored, planting of macrophytes is used as a tool to decrease turbidity, stabilize sediment, and decrease erosion, commonly implemented in deltas (Bakker, Sarneel, Gulati, Liu, & van Donk, 2013). Plants can be introduced as seeds or seedlings, but these life stages are not ideal for withstanding waves or flow currents (Sarneel & Soons, 2012). Therefore, whole plants or plant fragments are more commonly introduced (Bakker et al., 2013; Gonzalez, Sher, Tabacchi, Masip, & Poulin, 2015). Due to the positive and negative feedbacks acting on different spatial scales, a clumped planting may be more successful than an evenly spaced planting in tidal marshes (Silliman et al., 2015); this technique was first developed for tidal marshes, which can be found in deltas, but could also have implications for restoration further upstream, where similar feedbacks shape vegetation patches.

5 | CONCLUSION

River systems cannot be fully understood without incorporating the work of ecosystem engineers, which may act “selfishly” yet have profound impacts on the entire system, including physical characteristics and processes and ecosystem properties and function. In line with the hypothesis that there is a sweet spot for ecosystem engineering at intermediate disturbance and sediment supply levels (Corenblit et al., 2011; Gurnell, 2014), although ecosystem engineers actively influence geomorphic processes in a range of river environments, in terms of relative stability, channel width, and sediment size (Figure 2), they require some degree of dynamism to cause an alteration in sediment dynamics. Modifications of the physical environment commonly utilize sediment, and therefore sediment must be mobile yet not too dynamic, which can cause lethal effects on the engineering organism (Beveridge & Lancaster, 2007).

Further, we observed that the current literature is going beyond describing case studies of ecosystem engineers (e.g., given the recent publication of meta-analysis and reviews on this subject: Albertson & Allen, 2015; Hussner et al., 2017; Lecerf & Richardson, 2010; Romero, Goncalves-Souza, Vieira, & Koricheva, 2015; Statzner, 2012; Trinci et al., 2017). There are three exciting recent research trends.

1. *Ecosystem engineering effects on very long temporal scales.* Evolutionary geomorphology (Corenblit & Steiger, 2009) is an emerging field that aims to disentangle to what extent the river’s geomorphic features have controlled the evolutionary pathways of organisms. Or vice versa, to what extent have ecosystem engineers affected channel evolution of various river types?
2. *Ecosystem engineering effects on larger and smaller spatial scales.* A recent meta-analysis across ecosystems revealed that animal ecosystem engineers globally increase species richness (number of species) by 25% (Romero et al., 2015). In some cases, species richness may decrease locally but increase regionally due to increased landscape heterogeneity (Wright et al., 2002). Bioturbators do not create positive feedbacks at the scales that have been examined, but examination at smaller scales may reveal bidirectional effects of their biogeomorphic disturbances. Therefore, the scale of the effects is increasingly evaluated to understand biogeomorphic patterns and species distributions.
3. *Incorporation of ecosystem engineers into river management and restoration.* To date, only a few species have been documented as a tool for restoration, including beaver, willow, and some macrophytes (Pollock et al., 2014), and detailed methods for the use of beaver in restoration have been outlined in a handbook for practitioners (Pollock, Lewallen, Woodruff, Jordan, & Castro, 2015). However, there is potential for multiple other ecosystem engineers to be used systematically as a holistic tool for restoration in appropriate river systems; however, care should be taken so that ecosystem engineers do not become invasive in non-native areas, as with tamarix in North America and beaver in South America.

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CONFLICT OF INTEREST

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

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SUPPORTING INFORMATION

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