Received: 17 March 2022 | Accepted: 21 June 2022

DOI: 10.1111/1365-2435.14130

Functional Ecology BRITISH ECOLOGICAL SOCIETY

REVIEW

Ecosystem Engineers: Cross-scale and Cross-system Perspectives

Using ecosystem engineers to enhance multiple ecosystem processes

James E. Byers

Odum School of Ecology, University of Georgia, Athens, Georgia, USA

Correspondence
James E. Byers
Email: jebyers@uga.edu

Handling Editor: Maria Briones

Abstract

1. Ecosystem engineers (EEs) strongly influence ecosystems by affecting the abiotic properties of a system to which many biota respond. EEs can, thus, be pivotal species in restoration by helping to move systems toward desired states much faster and more efficiently than direct human intervention on the abiotic state.
2. For EEs to play a central, purposeful role in restoration, it is important to identify guiding principles about how the EEs may best be selected and incorporated.
3. I discuss three important aspects to determine (a) where the utility for EEs is high; (b) where EEs can most easily establish, are easy to handle and scaling-up their use is possible; and (c) how to recognize and value multiple, coupled and trait-dependent engineering functions of EEs.
4. Understanding these aspects of EEs should help guide purposeful and efficient choices in our approach to restoration.

KEYWORDS

ecosystem function, facilitation, foundation species, habitat-forming species, interactive effects, marginal utility, multifunctionality, non-native species

1 | INTRODUCTION

Ecosystem engineers (EEs) play a prominent role in ecosystems because they affect the abiotic conditions influential to the biotic community (Jones et al., 1994). By influencing the abiotic conditions, EEs alter context-dependent biological responses of resident species, which in turn influence energy flows and ecosystem functions. Ecosystem functions include the physicochemical and biological processes that occur within an ecosystem that influence life, many of which are directly linked to human well-being, such as carbon storage, productivity and nutrient cycling. The positive, but non-linear, effect of biodiversity on ecosystem functions is often attributed to the sampling effect, whereby more diverse communities have a higher probability of containing species that disproportionately boost ecosystem functions. EEs are surely a key category of species that drive the sampling effect due to their broad, outsized influence on the systems in which they are embedded. In a meta-analysis of EEs, Romero et al. (2015) found that the presence of EEs increases species richness by 25% on average, supporting that ecosystem engineering is a highly facilitative process. Thus, quantifying EEs and their influences within systems has become a central focus to understanding ecosystem processes and functioning (Gutierrez et al., 2011; Jones et al., 2010).

In addition to influencing natural ecosystem processes and functioning, EEs are also increasingly recognized as central to efforts to restore ecosystem processes that have been altered. Historically, many restoration efforts attempted to change the degraded abiotic state with the expectation that appropriate species and ecological processes will then recover (Palmer et al., 1997). Byers et al. (2006)

[Correction added on 17 November 2022, after first online publication: The Special Feature title has been corrected.]

argued to use EEs as a central focus of restoration efforts. This focus fits within the recent, broader recognition of using living organisms to do environmental work and engineering processes (Chapman & Underwood, 2011). For example, the U.S. Army Corps of Engineers has an 'Engineering with Nature' program, a large part of which focuses on using Natural and Nature-Based Features when conducting new engineering projects. 'Living shorelines' are a tangible example whereby an EE, such as a reef-building oyster, is used as an alternative to traditional coastal defence structures (e.g. bulkheads, seawalls), with the benefit that the living organism may keep pace with sea-level rise and provide co-benefits, such as habitat provisioning (Morris et al., 2019).

The benefit of the EE-centric approach is that EEs change the abiotic context of their environments, and thus may help to move systems toward desired states much faster and more efficiently than direct human intervention on the abiotic state. This approach taps into a larger idea of using alternative states and positive feedbacks to move systems in desired directions (Suding et al., 2004).

How often are EEs used as a focal point of restoration? Seemingly a lot, and certainly well before the term ecosystem engineering was coined in the 1990s (Jones et al., 1994; Jones et al., 1997). A historical reason for their widespread use was because EEs are often foundational species; thus, to restore a forest, trees were planted; to restore a coral reef community, coral were recruited. But what is unclear is the degree to which EEs were used explicitly for their role in affecting ecosystem processes, as opposed to being used solely due to their prominence in the system. It is conceivable that engineering was possibly not the leading reason for use of an EE, but rather, restoring with a foundational species yielded helpful, but not explicitly targeted 'side benefits', that is, the ecosystem processes, goods and services that EEs helped to facilitate. Increasingly, ecologists have argued that explicit recognition, or preferably, actual quantification of engineering functions of the species in a system, is helpful to enable predictions of how their presence collectively benefits a system (Cuddington et al., 2009). As a result, a strong quantitative case can be made for making EEs the intentional focus of restoration efforts.

An illuminating example of this is the Eastern oyster *Crassostrea virginica* that creates reefs in the intertidal (and sometimes subtidal) zone throughout much of its southern range from the mid-Atlantic states in the United States through the Gulf of Mexico and the Caribbean (Bahr & Lanier, 1981; Byers et al., 2015). For years, restoration focused on restoring and rescuing the fishery – building reefs for the sake of the oyster itself. However oysters engineer numerous ecosystem processes affecting the integrity and health of the estuaries in which they reside, including habitat provisioning for other commercially and recreationally valuable species, shoreline stabilization, erosion control, reduction of suspended particles and denitrification (Grabowski et al., 2020; Meyer et al., 1997; Newell, 2004; Peterson et al., 2003; Piehler & Smyth, 2011). Lenihan and Peterson (1998) and Lenihan et al. (2001) experimentally restored different shapes and positioning of oyster reefs to examine how the biogenic structure best modified hydrodynamics to provide optimal filter feeding conditions for the oysters and best protected newly settling generations of oysters from hypoxia. This work also documented the multiple influences of oysters as EEs because it quantified their role in providing habitat for other commercially valuable species. It was calculated that the engineering benefits of oyster reefs, including its habitat provisioning for other economically important fishery species, provided far greater economic benefit than the oyster's food value itself (Grabowski et al., 2012; Grabowski & Peterson, 2007). This recognition revolutionized the way the state of North Carolina approached oyster restoration. Now the state, and many others following their lead, use multiple factors in deciding where and when to build restored reefs.

In addition to the central roles of EEs, it is increasingly recognized that most ecosystems sustain multiple EEs that interact; yet only recently have their interactive dynamics been fully investigated (Altieri et al., 2007; Bishop et al., 2012; Gribben et al., 2019; Smith et al., 2018; Smith et al., 2021). These interactions may be key to the EEs' success, as well as producing important synergies that benefit ecosystem processes from the interactions of their engineering (Gribben et al., 2019), or antagonisms that diminish net processes (Berkenbusch & Rowden, 2003; Gamfeldt et al., 2013; Woodin, 1976; Zavaleta et al., 2010). Thus, EEs may be important players governing how changes in species diversity affect the provisioning of multiple ecosystem processes simultaneously, that is, the multifunctionality of ecosystems (Byrnes et al., 2014).

For EEs to play a central, purposeful role in restoration, it is important to identify guiding principles into how the EEs may best be selected and incorporated, and chart a strong empirically based approach for their use going forward. This may increasingly include considering the ability of EEs and their interactions with other EEs to affect multiple ecosystem services and processes. Thus, here I discuss three important conceptual considerations: (a) how the utility of engineering attributes is determined by the ecosystems and biomes in which they are embedded, (b) what factors make EE restoration most likely to succeed and (c) how to recognize and value multiple, coupled and trait-dependent ecosystem processes driven by EEs. Understanding these aspects of EEs should help guide purposeful and efficient choices in our approach to restoration.

2 | ABIOTIC CONTEXT GOVERNS THE UTILITY OF ECOSYSTEM ENGINEERS

Utility in economic terms is the usefulness to a system from the supply of a good – in this case an EE. I suggest that three primary factors affect the utility of an EE added to, or boosted within, a system: (a) whether the subsequent abiotic changes caused by an EE are relevant to the life histories of resident organisms; (b) the background environmental context, especially how much scope there is for change and how stressful the environment is (i.e. how much abiotic amelioration is needed); and (c) how much engineering is already being done by the same EE or another similar one in the system. The maximum utility will manifest when the EE provides a relevant engineering attribute, in a stressful environment, that is not presently supplied.

2.1 | Relevancy of ecosystem engineers to the life histories of resident organisms

Most all organisms are shaped by natural selection to fit the conditions of their environment. The physical environments of all ecosystems differ, and thus organisms' evolved life histories will vary predictably by ecosystem. For example, faunal inhabitants of a tundra will not be selected for arboreal living since the physical structure that makes that possible is missing from the ecosystem. Thus, addition of tall above-ground structure to such an environment (if it would even grow there) would be a foreign selective force, unlikely to aid many resident native species. The surest way to understand what EEs may be important to an ecosystem is to examine its physical properties and what engineering already occurs (or has recently gone missing).

Perhaps the most dramatic contrast to examine differences in abiotic conditions, subsequent life histories and expected effects of EEs is between terrestrial and aquatic biomes. These contrasts clarify the expectations of the physical modification you might seek or expect by EEs in each biome – not just in terms of restoration, but also in terms of the roles natural EEs are playing. Because the physics of water and air are so different, terrestrial and marine systems may exhibit fundamental differences in the ecosystem processes that are most modifiable, as well as in the sensitivities of species responding to modifications (Table 1). For example, the high specific heat of water buffers it from rapid temperature swings and suggests that engineering influences like shading will have higher utility and importance in terrestrial environments. Also, in terrestrial systems, few organisms spend their lives freely suspended above a solid substratum due to the enormous energy input required. The ecological engineering that tends to be important in terrestrial systems is structural support, which allows organisms to inhabit the third (vertical) dimension without tremendous energetic cost (beyond the initial investment in the engineering). Thus vegetation, spider webs and bird nests are important engineering for provisioning suspension-enabling structure for life in terrestrial realms. In contrast, due to water's high density, many aquatic species inhabit the pelagic zone, sometimes suspended for their entire lives with no structural aid. To be sure, engineered structure is still immensely important in both biomes, but it serves very different ecosystem roles for species. In terrestrial systems, as discussed, a primary role is structural support; while in aquatic systems the primary role is often for crypsis and predator refugia (e.g. Wright et al., 2014).

In addition, the abundance of life in the water column means that alteration of hydrographics can literally alter the flow and input of organisms to locations. Flow modification is one of the key physical alterations by EEs in aquatic realms. Flowing water upon hitting physical structure can be baffled, slowing water and allowing larvae to recruit to benthic habitats (Breitburg et al., 1995). Flowing water can also be channelled by physical structure into smaller volumes, increasing its flow speed (due to conservation of momentum) and enhancing food delivery, and thus growth of filter-feeding organisms that extract seston from the water (Lenihan, 1999). There are of course flow modifiers in terrestrial realms, for example, wind breaks, but because there are fewer biological elements occupying the vertical dimension, such modifications function more to alter temperature and evaporation than modify organismal flows and inputs (Cleugh, 1998). Intertidal habitats – where many nominally marine restoration activities occur – are a hybrid of marine and terrestrial systems. The system to which they most adhere depends on the specific tidal elevation and tidal amplitude.

In both realms, engineering done by infauna is important, but perhaps for slightly different reasons. In both, fossorial animals dig holes that turn soil, alter water percolation and provide refuges. On land, the holes also engineer temperature-buffered environments and alter water flow of surface runoff (Eldridge et al., 2009). In aquatic environments, burrows stabilize and aerate sediments, and their construction can increase the suspension (bioturbation) and thus bioavailability of deposited organic particles and nutrients (Volkenborn et al., 2009; Woodin, 1976). Burrowing and tube building (and the water pumping and irrigation that often accompany them) oxygenate deeper sediments and provide refuges (Gray, 1974; Reise, 2002; Rosenberg et al., 2001; Woodin, 1978).

Romero et al. (2015) found in non-tropical areas, EEs in aquatic environments had higher, positive effects on species richness than terrestrial systems. Specifically, EEs in aquatic systems increase species richness by 29.7%, whereas in terrestrial ecosystems, EEs boost richness just a few percent (~5%). This finding suggests that organisms in aquatic habitats are more sensitive to physical environmental alterations. Physical-biological coupling is certainly a strong area of research in aquatic realms lending support to this hypothesis (e.g. Byers & Pringle, 2006).

In sum, some common expectations for influential EEs and their characteristics differ by biome. In water, we expect EEs that modify flow, aerate sediment and provide structure for refuge. On land, we expect EEs that modulate temperature and provision structure for aerial support. In both we expect to see sediment stabilizers. Some of these categories match those of Berke (2010) who proposed a way to categorize EEs based on their functional similarities; she proposed four categories: structural engineers, bioturbators, light engineers and chemical engineers. Organizing EEs in such a way emphasizes that the function of engineers is most important and may be useful if we want to develop generalizations, including modelling approaches of the effects of EE on systems (Cuddington et al., 2009; Hastings et al., 2007; Yeakel et al., 2020).

2.2 | The importance of background physical context

A differential influence of an EE between systems could result because the engineering attribute is more important in a different

TABLE 1 Some of the physical and chemical differences between water and air, the implications of these differences for the biology of organisms and the relative differences in the degree and kinds of ecosystem engineering expected as a result

Properties of water relative to air	Biological implications for aquatic organisms	Ecosystem engineering implications
High specific heat and high heat of vaporization	Maintain uniform body temperatures conformed to environment	Heat buffering from shading not as important as on land
High surface tension	Makes floatation easier	Structural support is unnecessary
High viscosity	Easy flotation (for small organisms)	Flow modifiers will have large effects on organisms living in water (inhabiting third dimension)
High dissolving power, high in dissolved solutes	Chemicals easy to mix and transport	Easy to chemically alter the environment
High conduction of heat	Less heterogeneity in temperature; objects have aprroximately same temperature;	Ecosystem engineers that provide thermal refuge are uncommon
High density	Cost of inhabiting third dimension is low (dense body masses supported); cost of transport higher; sound transmission fast	Structure is important for protection, but not as a buoyancy aid – see above
High light absorbency	Low to no light at sufficient depth	Bioluminescence common
Low oxygen concentration	Need adaptations to deal with low O_2. Or organisms could associate with areas with higher flow, higher O_2 gradients and lower temperatures (that hold more dissolved gas)	Flow modifiers, bioturbators and O_2 provisioners are influential. Burrowers aerate hypoxic sediment

environmental context (Moore, 2006; Wright et al., 2002). As an example, a beaver dam will have a larger influence if built in a stream of fast flowing water, as opposed to a pond that already has extensive surrounding wetlands. The scope for engineering-induced change is much greater in the former scenario because the flow speed of the water can change by a much greater velocity and create an adjacent habitat that is at present minimally existent (Figure 1).

Menge and Sutherland (1987) developed a conceptual model that provided a framework to categorize how ecological processes varied in their importance to community structure along a stress gradient. Specifically, the Menge-Sutherland model predicted that under high recruitment, across a gradient of increasing environmental stress, the most important community-driving variable will shift from predation to competition to abiotic stress (Figure 2). Thus, it is thought that EEs will correspondingly vary in their roles and importance across environmental gradients, with EEs more influential in harsh/stressful environments where facilitative effects resulting from their environmental alteration and amelioration have more relative, if not essential, value (Figure 2; Crain & Bertness, 2006). For example, in the Negev desert, the survival of several plant species is predicated on the engineering performed by microbial crusts that generate and collect precipitation runoff, thus concentrating sparse rainfall into a sufficient amount to be biologically meaningful (Shachak et al., 1998). In the same vein, the meta-analysis by Romero et al. (2015) on EEs across systems found that in terrestrial ecosystems, engineers displayed stronger positive effects in arid environments (e.g. deserts). Harsh environments give habitat ameliorating EEs higher utility because these environments have a larger scope for environmental change. Thus, alleviation or alteration of environmental conditions at the margin of survivability will have the largest influence on biota.

2.3 | The influence of ecosystem engineer density

Marginal utility is the economic term that describes how much benefit accrues from the addition of another individual unit of a commodity. As more EE individuals are added to a system, there will typically be less marginal utility (diminishing returns) in the engineering performed (Moore, 2006). After sufficient additions, the system will be saturated with engineering. But even before reaching that asymptote, the engineering of the added EEs will likely begin to overlap with each other, and the EEs themselves might begin to interact biologically, for example through competition, which would likely result in a decelerating accumulation of engineered attributes up to the asymptote (Figure 1). Thus, if an EE is in short supply, its marginal utility is high. As a simple illustration, a beaver dam is far likelier to

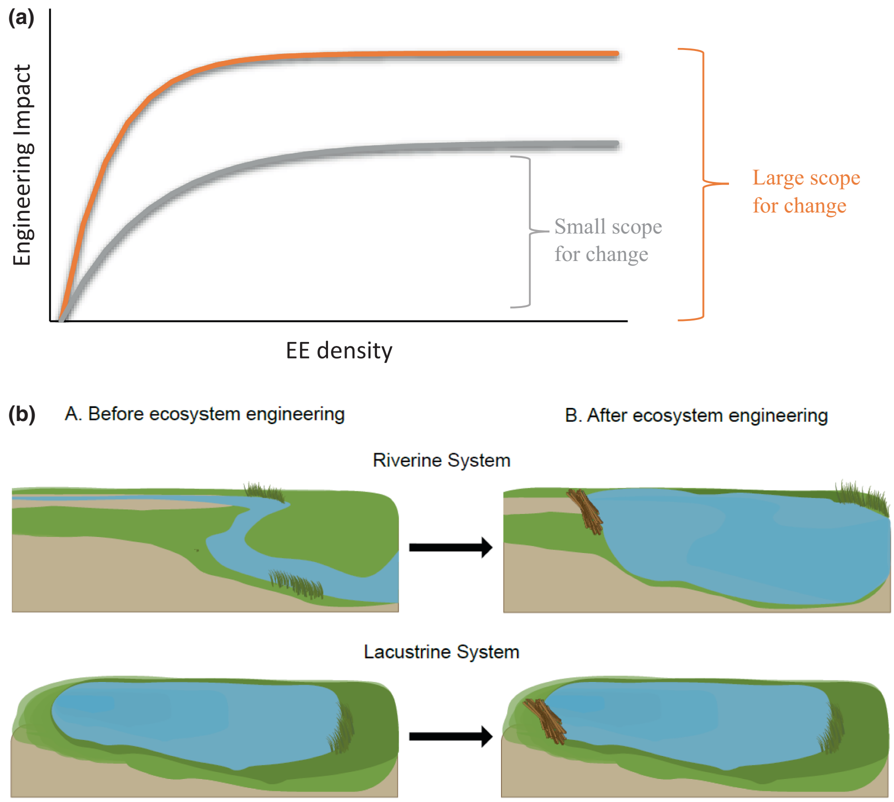

FIGURE 1 Effects of ecosystem engineer (EE) density and environmental context on engineering impact. (a) The two curves represent environments with different scopes for environmental change based on their present abiotic states. The asymptote reflects the maximum amount of influence, or the scope of change, possible for a system property. The environment denoted in orange has a large scope for physical change, and the grey line represents an environment with less scope for physical change. As an example, the orange line could represent a river with a fast current being blocked by beaver dams, and the grey line could represent adding beaver dams to a lake system which has a slow current. In both cases increasing EE density increases engineering impact by slowing water flow, but the marginal utility is greater in the river habitat. The scope for change within a system diminishes as more engineers are added to it and it approaches its asymptote. (b) A comparative illustration of the influence of the ecosystem impact from a beaver dam in a fast-moving stream (top row) and slow-moving lake (bottom row).

have large marginal impact in a watershed where it is the only one, compared to a watershed where it is one of a hundred. Keep in mind that some EEs must reach a critical mass of individuals before substantive engineering can occur (e.g. termites amassing to create a colony and mound, or oysters creating a reef). In these cases, the relevant unit of density is likely the engineering structure, that is the number of termite mounds or reefs, and not the number of individual engineers themselves. Ultimately, the relative impact of an EE (or EE structure) is greater when the EE is rare.

As an example of this effect in a restoration context, Geraldi et al. (2009) added oyster reefs to three of six tidal creeks expecting to see a boost in diversity and abundance of estuarine species responding positively to the habitat provisioned by the EE. Surprisingly, the reefs did not have predicted effects as had previously been seen in other similar systems. Upon closer examination, the authors determined that the lack of change was likely due to a small scope for change because many habitat provisioning EEs were already present in the surrounding salt marsh system. Thus, presumably at a larger landscape scale, the environment was already saturated with EE function (the asymptotic portion of Figure 1). This example illustrates that redundancy of engineering effects can result not only from an increase in the density of a single focal EE species, but also from overlapping functional groups of other existing EEs. An important side note is that the redundancy occurred in the functions they were sampling for – biodiversity and abundance of estuarine organisms. However, having both oyster and marsh habitats may provide differences in other (unmeasured) functions. This possibility of EEs with multiple influences is discussed in further detail in the section: *Coupled ecosystem processes driven by EE*, below.

3 | FACTORS AND APPROACHES THAT MAKE ECOSYSTEM ENGINEER–CENTRIC RESTORATION MOST LIKELY TO SUCCEED

The EE-centric approach to system restoration makes sense because it allows EEs to perform the hard work of moving system

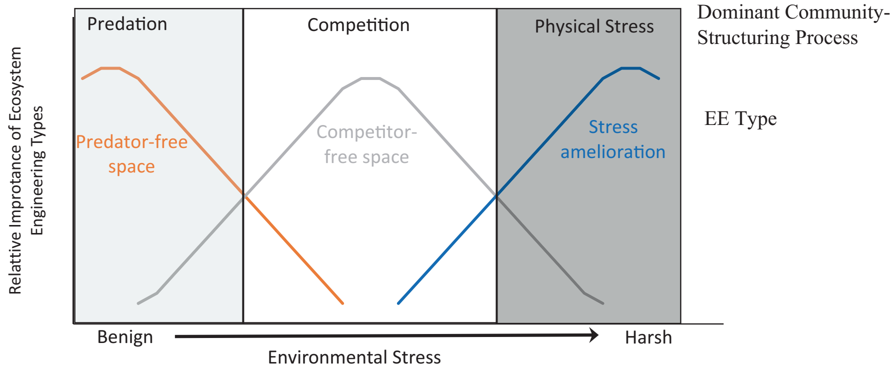

FIGURE 2 Relative importance of three broad types of ecosystem engineering identified by Crain and Bertness (2006) across an environmental stress gradient. The three boxes indicate dominant community-structuring processes predicted by the Menge and Sutherland (1987) environmental stress model. Ecosystem engineers (EEs) that affect and alleviate the predominant of these dominant factors will be the most important in structuring community processes in environments along the stress gradient (the engineering functions and their accompanying labels are colour-coded). The rightmost box, where physical stresses dominate, is the only one where EEs are essential, through their physical alterations of the environment that alleviate stress. In the left and center boxes, EEs can provide predator and competitor refugia respectively, serving to increase biodiversity and ecosystem functioning. Modified from Crain and Bertness (2006).

states. However, in some cases the EEs may need some help (Guiden et al., 2021). For example, certain ecosystem properties (e.g. community composition, abiotic factors) could be manipulated to increase the proportion of certain EEs, which boost their attendant cascading effects on ecosystem functioning (Boogert et al., 2006; Byers et al., 2006). Or the proper selection of the best EE, or the best combination of EEs, may engender the most restoration success.

3.1 | Where is boosting or establishing ecosystem engineer the easiest?

As discussed above, a single EE (or engineering structure) typically has the most marginal influence, but higher densities of EEs still tend to lead to increasing levels of *absolute* amounts of engineering. The best scenario for EE-centric restoration is when an influential EE already exists and one only needs to boost its density. These are cases where you just have to get a species over a low density hump and then positive feedbacks often take over for sustaining and promoting the species (Silliman et al., 2015). Most commonly this might result from an Allee effect (Armstrong & Wittmer, 2011). EEs typically exert positive feedback on themselves. Such positive feedback can be lacking in the establishment phase if its densities are too low. For example, there will be exponential increases in propagule production as a population grows. But other positive feedbacks also can occur due to group living benefits, for example in reef-building organisms like oysters, or colonial species like coral. Oysters are gregarious settlers and need established adults to produce settling cues (Bahr & Lanier, 1981). Mangroves need enough established adults to help ensure quiescent hydrology for recruitment (Smith et al., 2018). Dominant trees in tropical rain forests have extensive mycorrhizae networks that can promote positive density-dependence in the area adjacent to the parent tree, facilitating self-recruitment (Zahra et al., 2021).

Boosting or establishing EEs will also be easier in systems with no hysteresis, and thus moving the system state is not hard (Byers et al., 2006). When systems become entrenched in an alternative stable state, it can take far more energy and input to flip the state to the desired alternative (Suding et al., 2004). On the other hand, EEs may be the best bet for moving a system in hysteresis. Laying down bivalve shell may overcome hysteresis due to the lack of settlement cues and spur natural recruitment of mussels (Capelle et al., 2019). Once adults have established, the system becomes self-sustaining in EEs. As another example, certain places in Western Australia's drylands have a severe problem with soil salinization. The problem is very difficult to correct with mechanical means, and even finding the right means of biological remediation has been difficult. A solution involving a few species of specific EEs is proving to work. Specifically they have established salt-tolerant (halophyte) trees and shrubs with a variety of rooting depths. These have promoted the downward movement of, and the even distribution of, salts in the soil profile while lowering the water table (Barrett-Lennard, 2002). However, the initial establishment of these species is not easy and can initially require substantial human assistance (Pannell & Ewing, 2006).

Three final straightforward considerations that emerge from all of the above examples are as follows: (a) As suggested from Section 2, consider systems with the largest scope for increase in engineering impact. Those systems not already at equilibrium or full of EEs will be the most sensitive to EE additions. Furthermore, if a system is already full of EEs it would likely not need boosting/restoration. (b) Proper abiotic conditions for EEs to exist and thrive are essential. If these conditions do not naturally exist, good gardening and animal husbandry techniques may be required to make conditions optimal (Silliman et al., 2015). Prepping the environment for the cornerstone EEs should be a priority because they should ideally be the first to be established. (c) Species ideally should be easy to grow, propagate and handle so they can be readily outplanted into the environment.

3.2 | Identifying pivotal ecosystem engineers in ecosystem restoration

Perhaps because they meet many of these characteristics, the pivotal, focal EE species in marine systems for restoration have been limited to a small number, especially in comparison to terrestrial systems. As in most systems, structure-provisioning, foundational species are key controllers of ecosystem processes. For marine systems, almost all of the attention is focused on five species groups: saltmarsh cordgrass (usually *Spartina* sp.), oysters, coral, mangroves and seagrasses. There are a few other species in immediately proximate systems like dune-stabilizing plants (sea oats) but those live in a predominantly terrestrial system. Each of these autogenic EEs has a huge literature on their roles affecting ecosystem processes, especially habitat provisioning. All are shallow, nearshore, ecosystem-defining species. From a restoration perspective they are natural foci not only because of their central roles, but also because, with possible exception of coral, they are easy to work with. They live nearshore, can often survive out of water for periods and can tolerate handling stress (mangrove seeds, e.g. are viviparous and require no germination).

As evidence that the intensified focus on these few species is not unfounded, throughout most of the US Atlantic and Gulf coast estuaries, two species from this group of five – the marsh cordgrass Spartina alterniflora and the Eastern oyster *C. virginica* – predominantly control the functioning, stability and diversity of the system. Specifically, these species control sedimentation rates, affect erosion rates, buffer upland runoff and provide biogenic habitat. Oyster reefs also filter water and provide refuges for economically valuable species (Grabowski & Peterson, 2007). Their strong, combined influence on multiple properties and flows within ecosystems exemplifies their major influence on system integrity (Koch et al., 2009). If the ecosystem services produced by these species were removed, they would be very costly and perhaps impossible to replace (Barbier et al., 2011).

These pivotal five species groups have been the basis for some massive scale restoration projects. The billion oyster project seeks to restore this critical EE in NY Harbour involving thousands of school children in the process as part of an education and outreach component (https://www.billionoysterproject.org/). The goal is not primarily to produce a food resource, but rather to harness the oysters' engineering abilities to reduce storm surges and enhance water quality. In Senegal, several non-profits, including the Senegalese NGO Océanium, have organized community groups into the world's largest mangrove reforestation, planting more than 79 million mangroves over the last decade (https://livelihoods.eu/portfolio/oceanium-senegal/). The Coral Restoration Foundation working in the Florida Keys has seven offshore nurseries where they rear 11 species of coral. Since 2012, they have outplanted >120,000 corals from their nursery to 17,500 m^2 (https://www.coralrestoration.org/).

This small collection of focal species for marine EE-centric restoration is seemingly a much narrower palette than for terrestrial EE-based restoration. In terrestrial systems, the variation in EE choices spans from Gopher tortoises, which dig holes in landscape, to trees for wind breaks and fog collection, to microbial crusts which affect runoff in the Negev Desert (Eldridge et al., 2002; Shachak et al., 1999). Coggan et al. (2018) reviewed studies of terrestrial animals as EE. They were interested in the taxonomic representation and documented ecological functions of engineer species including burrowing, soil manipulation, nest building and plant manipulation (i.e. non-trophic actions that modify plant structure, e.g. by curling leaves for shelter). They found 122 engineer species representing 28 orders across four taxa – mammals, birds, reptiles and invertebrates. Burrowing mammals were the most common (27% of studies). Terrestrial vegetation is an even larger group, with revegetation and afforestation as the predominant methods. Among other effects, these projects often seek to reduce soil erosion, decrease desertification, sequester carbon or regulate hydrology. Cui et al. (2021) analysed 962 studies documenting restoration projects in China over the last four decades. They found the projects were almost all terrestrial or riparian, and because they occurred across more than 50 different ecosystems, presumably used many different plant species.

Regardless of the biome, identifying EEs and engineered habitats that are essential for protection, preservation and restoration is critical. All species engineer just as all species eat and compete. So the key is determining the kind and degree of engineering each species is doing and which is most important and influential on the system. Once this is delineated, start with the biggest, most influential EEs – not all are created equal, and specific species choices can matter. For example, the aforementioned Eastern oyster, *C. virginica*, is reef-building, whereas, the most cosmopolitan oyster *C. gigas*, which was spread globally for aquaculture (Ruesink et al., 2005), is not. If one cared solely about food production, *C. gigas*, which is big and grows quickly, might be the focus of an introduction effort. If ecosystem processes are central, then a reef-builder like *C. virginia* would be.

It is important to note that influential EEs may include not only the pivotal ones discussed here, but also those with negative influences. The latter case often arises if an EE attribute is too foreign to a system, then it often boosts invasive species that benefit from the novel engineered attributes (Crooks, 2002; Emery-Butcher et al., 2020). By providing abiotic properties outside the realm of that to which the native species are adapted, an introduced structure or EE can differentially aid non-native species since the altered abiotic environment erases the advantage of local adaptation normally accrued to native species due to their long term incumbency. This is known as selection regime modification (Byers, 2002) and is an explanation for how rapid environmental change might disfavour native species that previously would have been locally adapted. For example, in many sedimentary estuarine environments, hard surfaces are rare. When humans place hard substrates such as docks, rip rap and boats inside soft-sediment embayments, non-indigenous fouling species can be common on those substrates (Stachowicz et al., 2002; Tyrrell & Byers, 2007; Wasson et al., 2005). Within soft-sediment dominated Elkhorn Slough, California USA, Wasson et al. (2005) found an approximately equal number of species in soft and hard habitats; however, exotic and cryptogenic species comprised 38% of species in soft sediment and 68% on hard substrates. Furthermore, non-native taxa covered the vast majority of space (84%) on the human-introduced hard surfaces. This idea is further supported by Romero et al.'s (2015) meta-analysis finding that EEs that create new habitats or microhabitats had stronger effects than those that simply modify habitats (Romero et al., 2015).

4 | COUPLED ECOSYSTEM PROCESSES DRIVEN BY ECOSYSTEM ENGINEER: MULTIFUNCTIONALITY AND MULTI-INFLUENCE ENGINEERS

In any given system there are multiple biological ecosystem processes, such as productivity, carbon cycling and decomposition, that are highly influenced by physical factors. The influential role of the physical environment on the biological processes emphasizes the context dependency of these ecosystem processes, as well as highlighting the potential roles for EEs to affect them. These ecosystem processes used to be considered singly, but increasingly the provisioning of multiple processes simultaneously or multifunctionality, has risen in prominence (Byrnes et al., 2014; Manning et al., 2018). One of the central tenets of the work in ecosystem functioning is that the provisioning of multifunctionality, or even the quantity of a single ecosystem process, rises as species diversity rises. The positive relationship between biodiversity and ecosystem functioning has been shown to often be driven by the sampling effect, whereby increases in species richness increase the odds that the collection of species will contain a highly influential species (Huston, 1997; Tilman et al., 1997). Those highly influential species are often likely to be EEs, since by affecting physical properties of their environment they broadly affect the biology of the system.

Some of the best evidence for multifunctionality stemming from EEs, especially in terms of effects on species diversity, comes from recent modelling work by Yeakel et al. (2020). The authors examined community assembly in ecological network models. They found that increasing the number of EE species increases stability and decreases extinction. Having only a few EEs led to many extinctions and instability, whereas many EEs led to stability and few extinctions. Essentially, increasing the number of engineers increased the redundancy of the engineers, and this tended to stabilize the system. Thus, EEs may both boost diversity while also increasing persistence by facilitating colonization and limiting competitive exclusion.

In fact, certain EEs are so influential that even alone they can affect multiple abiotic properties of a system that in turn affect multiple ecosystem functions. I call these multi-influence engineers, and they should tend to be the most impactful species in a system. The five pivotal groups of EEs used in marine restoration mentioned above are all prime examples, with each affecting everything from sedimentation rates to habitat provisioning to water flow. If multiple processes are influenced by an EE, an interesting question to ask is whether there is disproportional strength or importance of the processes affected, for example, is the habitat provisioning by an EE more valuable than its effect on sedimentation? Thus, even if a species is a multi-influence engineer, its effects on various abiotic factors and resultant ecosystem functions may differ in magnitude or importance. As an extreme example, there are even interesting cases where a single species can have multiple engineering influences that act in opposing directions, facilitating and hindering species at the same time. One must consider the strength of effects of the multiple engineering process and potential synergies and tradeoffs among them. For instance, burrowing ghost shrimp aerate sediment, increasing circulation and flow beneath the surface, thus making the shallow sediment hospitable for many aerobic organisms. However, in the process of burrowing, they also bioturbate, and the resuspended sediment hinders filtration by filter feeders and photosynthesis by algae and plants (Berkenbusch & Rowden, 2003; Woodin, 1978). Recognizing that most species are (or have potential to be) multi-influence EE, it is important to ascertain the range of potential effects of an engineer in the setting where it will be used.

Additionally, as species diversity rises, and EE species diversity along with it, there can be important interactions between the EEs and other species, or between the EEs themselves, producing synergistic or antagonistic interactions that influence their engineering. Synergistic examples include: *Spartina* and oysters, whose engineering in southeastern US estuaries was described above, interact and facilitate each other. At the mid-tidal elevation where the populations of the two species abut, oysters harden the shoreline and stabilize sediment protecting *Spartina* from erosive hydrologic energy, while *Spartina* shades juvenile oysters aiding their recruitment, survivorship and growth (R. D. Harris, personal communication). In addition, because coral species can have very different morphologies (e.g. branching and crusting), multiple species with complementary forms make more complex 3D habitat structure. Fish communities differ drastically based solely on the basis of dominant corral composing a reef (Komyakova et al., 2018).

Examples of antagonism between EEs appear less numerous in the literature, but in theory they should abound. Coral build structure and parrotfish chip it away; trees build structure and beavers tear it down, in this case to make another structure in an adjacent, aquatic system. Or EEs may mutually exclude one another when competing for space, and in so doing impose their own engineering that differs in kind or degree. To illustrate, if one species of tree replaces another and the trees differ in their engineering capacities, the replacement of one tree species by another will ramify to affect the ecosystem. A recent example of this scenario in restoration is currently affecting Miami Beach, Florida. To reduce the heat island effect, the city seeks to drastically reduce the number of palm trees over the next few decades in favour of trees like maples and oaks that provide better shading and carbon storage (Allen, 2022).

Sometimes the EEs not only interact, but there is a dependency of the EEs on one another, referred to as hierarchical engineering. For example, experiments in Australia examined the EE alga *Hormosira* *banksii* that is important for its habitat structure. Bishop et al. (2012) showed that when the alga wraps around mangrove roots, another structurally important EE in the system, this promotes a multiplicative boost in species richness than from either EE alone. Presumably this effect results from an enrichment of habitat heterogeneity. Facilitation cascades are a more generalized version of this concept where one species benefits another in a chain of positive interactions, and thus is an area where synergies abound. Facilitation cascades are not restricted to EEs, but they are often some of the more influential species involved (Altieri et al., 2007; Gribben et al., 2019; Thomsen et al., 2010).

4.1 | Restoring multi-influence and interactive ecosystem engineers will have large effects

Because of the outsized effects of multi-influence EEs and those involved in important synergistic interactions, restoration with these species should be highly impactful. Living shorelines used to bolster coastal shoreline defence are a good example (e.g. Morris et al., 2019). Sometimes the goal is singular (e.g. to reduce erosion); however, other ecosystem processes are boosted because they are part of a suite of processes that the EE affects that are bundled together. For example, a living shoreline built of oyster reef may be installed to prevent erosion. Oyster reefs harden the shoreline, but they also provide habitat and water filtration. That is, even if a multi-influence EE is restored for a single ecosystem process, or even no processes, but rather, for an ecosystem good (such as mangroves for wood or oysters for food), there still will be concomitant changes in the bundled, inseparable abiotic factors and ecosystem processes that the EE affects in the system.

This push for species that have outsized influence has been a motivating force behind the development of the Engineering with Nature (EWN) movement (https://n-ewn.org/). EWN seeks to harness natural engineering processes and align them with engineering goals to deliver sustainable economic, environmental and social benefits. The emphasis on natural infrastructure to perform engineering functions and services, including a broad array of social, environmental and economic benefits, such as flood protection, recreation opportunities, support of economically valuable species, and absorption of pollution and carbon dioxide means that multi-influence EEs are often the central focus of EWN projects. Jetties built out of oyster reef and out of concrete will both slow the flow of water (Dugan et al., 2018). But the oyster reef also engineers further abiotic modifications. Additionally, the oyster reef can grow, and thus repair itself and adapt to the local environment.

An important lesson from all of this is that pivotal EEs are those that affect multiple processes simultaneously and those that interact to jointly produce physical changes with attendant ecosystem effects. Thus, identifying which EEs are part of hierarchical engineering or synergistic interactions seems important for restoration (Angelini et al., 2016; Derksen-Hooijberg et al., 2018; Gagnon et al., 2020). It may mean that restoration of multiple EEs is important. In addition, it could mean that protecting a single EE could have multiple benefits by keeping synergies intact. All the interactions of EEs and their resultant physical alterations and resultant multifunctionalities are not always known, let alone quantified.

4.2 | Novel and multiple influences can lead to problems with non-native ecosystem engineers

As discussed above, many impactful non-native species are EEs (Byers & Grabowski, 2014; Crooks, 2002; Sousa et al., 2009). This follows logically from the fact that EEs by definition are those that affect the abiotic environment, which in turn influences every species that lives there. Examples include the following: beaver *Castor canadensis* in Patagonia; kudzu *Pueraria montana* strangling trees in North American forests; *Ficopomatus enigmatus* tube worm reefs in coastal bays of Argentina and western North America; *Agarophyton* (formerly, *Gracilaria*) *vermiculophylla* seaweed on mudflats of the southeastern United States and Europe; water hyacinth *Eichhornia crassipes* covering entire lake surfaces (Byers, 2009; Byers et al., 2010; Crooks, 2002; Emery-Butcher et al., 2020; Forseth & Innis, 2004; Haram et al., 2018; Rilov et al., 2012). However, certain native species may respond positively to the system-wide changes wrought by the invasive EEs. A meta-analysis of invasive marine EEs revealed that although their overall effect on ecosystem functions was small and negative, positive effects were not uncommon (Guy-Haim et al., 2018). Similar findings were produced from a review of freshwater invasive EEs (Emery-Butcher et al., 2020).

There have been cases where scientists and practitioners have promoted the use of non-native EEs, for example in situations where a native EE was no longer an option (e.g. Leuzinger & Rewald, 2021; Schlaepfer et al., 2011). The promoters argue that the ecosystem processes that the EE influences may outweigh the negative (or unknown) effects that the novel species brings to the ecosystem. Such a proposition requires a high burden of proof given the high impact of invasive EEs (Byers & Sotka, 2019; Sotka & Byers, 2019). It is tempting to think a non-native EE affects all the right, desired processes and nothing more. But the commonality of multi-influence EEs suggests this will rarely be true. For example, a nitrogen-fixing plant may be introduced for that specific function – to aid a nutrient poor system (e.g. Koutika et al., 2021); however, because of its multiple influences, one has to also consider that the tree engineers its environment in other ways such as shading, adding allelochemicals to the soil, blocking wind, etc. Once considering all of the collective engineering functions of a species, very rarely will the multiple functions of a non-native EE match a native analogue exactly. Furthermore, even if no ecosystem engineering functions have been overlooked and the known processes the novel EE affects are similar in kind, they can be of grossly different magnitudes (Cavaleri et al., 2014). Because of their outsized influence and their precedent of causing great environmental impact, non-native EEs should be approached with extreme prudence, if at all. More likely, they should be targets for elimination rather than addition because of their large, and often novel, environmental alteration. If engineering was important in a system historically, presumably there is a native EE that could be promoted for restoration or reintroduction.

4.3 | Legacies and trait-dependent engineering increase the influences of ecosystem engineers

Morphological, physiological and behavioural traits differ between species, including EEs. Traits of an EE – both when alive and as part of its legacy effect after death – can strongly affect its abiotic influences, as well as its interactions and synergies with other EEs. Furthermore, because legacy effects and traits of EEs can change over time, EEs can manifest multiple temporal influences. An underdeveloped area of research in EEs is how their traits influence the strength of their engineering, and in turn their influence on community structure and function (Badano & Cavieres, 2006). This could be an important and influential aspect, judging from the limited studies that have investigated it. For example, Schutte and Byers (2017) examined the epibiotic community that is composed of sessile marine organisms (largely sponges) that live on the subtidal portions of aerial mangrove roots. These roots, which are a key structural EE, grow downward from limbs of the tree toward the ocean floor; within a population there is variation in roots that are contacting the bottom and those which are dangling in the water column. They found that the simple trait of whether a root contacted the bottom greatly affected the epibiont community growing on it. Mechanistically this difference arose because those roots touching the bottom provided physical access for predatory sea stars, and their subsequent predation greatly changed the sponge community composition; those roots that were off the bottom were protected from sea star predators. Because the affected sponges are also themselves important engineers, the hierarchical effects of this simple mangrove root trait is further magnified.

As another example, of trait-dependent engineering Bishop et al. (2009) identified traits of an alga *Homosira banskii* that engineered habitat for molluscs. Algae that had larger vesicles and longer thalli, supported 200% more molluscs. Interestingly, these algal traits were plastic, and algae from the estuary had more of these preferred traits than algae from the outer coast. Thus, not only do traits of EE matter, but the traits themselves can be plastic, under environmental control. The striking insight is that the influence of EEs at the community level can be mediated through their traits, which are themselves dependent on environmental conditions (Bishop et al., 2009).

A similar example is seen in the dune grass, *Ammophila breviligulata*, that lives throughout the Great Lakes region, where it is an important stabilizer of sand dunes. Two traits of the plant – its tiller size and density – are important determinants of how effectively it stabilizes sand and builds dunes (Hacker et al., 2012; Zarnetske et al., 2012). Emery and Rudgers (2014) identified that multiple environmental factors including temperature, precipitation and latitude affect tiller size, while soil organic matter affects tiller density. Thus, traits influence the engineering of an important dune-building species, and these traits themselves are environmentally influenced.

Trait differences collectively contribute to the type and magnitude of physical alteration that an EE performs. If the type and magnitude are sufficiently different from other EEs, this leads to a degree of uniqueness that can be a major part of an EE's influence. For example, like dozens of marine infaunal species, *Diopatra cuprea* worms build tubes on mudflats helping to stabilize and aerate sediment (Berke, 2012; Myers, 1972). But uniquely *D. cuprea* decorates its tubes with surrounding objects, and in so doing, attaches and facilitates seaweed species, especially the non-native seaweed *Agarophyton vermiculophylla*, by anchoring it in place in a highly sedimentary environment (Byers et al., 2012; Thomsen & McGlathery, 2005). It also does this anchoring at an intertidal height that provides an optimal balance of moisture and sunlight for the attached *A. vermiculophylla* seaweed (Kollars et al., 2016).

Contributing to their overall multiple influences, a final *postmortem* effect that EEs can have is their legacy effects. Some EEs, especially those with calcified structure like oysters and coral, influence the abiotic environment similarly when dead as they do when alive (Hastings et al., 2007). Termite mounds may persist for thousands of years, and beds of marine mollusc shells for millions (Kidwell, 1986; Moore & Picker, 1991). However, in most cases, without biological maintenance of the stature and shape of an engineered structure, it degrades over time, altering its traits, and thus its influence on the physical environment and the biology of the system. How the influence of engineering decays with the structural legacy over time is an area ripe for future work. Furthermore, live and legacy effects of EEs may differ not only in degree but also in kind. For example, the marsh cordgrass *Spartina* when alive performs the many ecosystem services discussed above. When dead, the grass stalks are buoyant and are often delivered and stranded within high intertidal marshes (Valiela & Rietsma, 1995). The dead vegetation, which is known as wrack, requires many months to decay in part due to its high lignin content (Currin et al., 1995). Furthermore, even though individual grass stalks eventually decay, the wrack itself can be trans-generationally persistent, because of its constant production and delivery. The wrack can smother vegetation underneath it, leach nutrients and provide habitat for nest building species. Thus, the legacy engineering effect of *Spartina* wrack often has strikingly different effects from its live counterpart due to differences in orientation, location and traits (Smith et al., 2018, 2021).

Legacy studies are a way to study natural temporal variation in trait-based influences of EEs. A more immediate, experimental approach to parse effects of traits on EE outcomes is structural mimic studies (Crooks, 2002; Tait et al., 2020; Wright et al., 2014). Thus, mimic studies, can be a powerful way to understand the mechanisms of the effects of EEs and the contexts of their influence, and can thus help inform restoration choices. Mimics are usually inert structures that simulate the physical structure of the focal organism divorced from any of its biological influence (Jones et al., 2010). For example, Crooks (1998) and Crooks and Khim (1999) used fibrous plastic mats to mimic mats made by byssal threads of the mussel

Musculista senhousia that greatly boost the benthic invertebrate community of intertidal mudflats. Comparing these two treatments the authors could parse how much of the effect of the mats was through their physical engineering (habitat provisioning, alteration of flow and sediment) versus a biological aspect such as serving as a food source. Mimic experiments can target even more precise parsing of ecosystem processes performed. Smyth et al. (2016) built experimental reefs of live oysters, reefs of dead shell only and mudflats without shell to compare how sediment nitrogen cycling was influenced by the physical structure and the biological activity of oyster reefs. By comparing a dead reef to a regular live reef they could separately quantify ecosystem processes performed by the oyster reef that were due to purely structural effects on flow and sedimentation and those due to filtration effects on clarity and denitrification of the water, which only the live oysters could perform. In a similar vein, Lenihan et al. (2001) built oyster reefs of different shapes and sizes to understand how the physical structure affected flow rates and subsequent biological community composition and resilience to disturbances like hypoxia.

5 | CONCLUSIONS

Enhancing the success of EE-centric restoration in essence centers on identifying the best-suited habitats and species. As discussed here, three critical considerations guide the choices of species and prioritization of places. First, identify places where utility is high. This will occur most often in systems that have high environmental stress, where the EE provides a relevant engineering attribute that is presently supplied in low quantity. However, completely novel engineering, for example from a non-native species, is usually bad because it is outside of the evolutionary history of native, resident organisms, and thus likely to attract and encourage non-native species from other systems. Second, focus where EEs can most easily establish, where the EEs are easy to culture and handle, and where scaling-up is possible (e.g. the Billion Oyster Project). Third, remember that not all EEs are created equal. Multi-influence EEs and those EEs that are part of multifunctionalities and synergies usually have the farthest reaching effects in a system. Also, as part of an EE's influence, evaluate the effects of its legacies and traits (such as size, age, density). The influence of these latter aspects of EEs on their functioning within a system present the biggest knowledge gaps, and thus the greatest potential to inform EE ecology. Collectively these considerations should help guide efficient and sustainable EE-centric restoration.

ACKNOWLEDGEMENTS

Thanks to Maria Briones, Shelby Ziegler and Matt Pierce for constructive comments on this manuscript.

CONFLICTS OF INTEREST

None to declare.

DATA AVAILABILITY STATEMENT

There are no additional data to accompany this manuscript because as a conceptual review paper, all data are included in the manuscript.

ORCID

James E. Byers https://orcid.org/0000-0001-9240-0287

REFERENCES

Allen, G. (2022). *Florida cities ask: Are there too many palms?* National Public Radio. Retrieved from https://www.npr.org/2022/01/05/1064876188/

Altieri, A. H., Silliman, B. R., & Bertness, M. D. (2007). Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. *The American Naturalist*, *169*, 195–206. https://doi.org/10.1086/510603

Angelini, C., Griffin, J. N., van de Koppel, J., Lamers, L. P. M., Smolders, A. J. P., Derksen-Hooijberg, M., van der Heide, T., & Silliman, B. R. (2016). A keystone mutualism underpins resilience of a coastal ecosystem to drought. *Nature Communications*, *7*, 12473. https://doi.org/10.1038/ncomms12473

Armstrong, D. P., & Wittmer, H. U. (2011). Incorporating Allee effects into reintroduction strategies. *Ecological Research*, *26*, 687–695. https://doi.org/10.1007/s11284-011-0849-9

Badano, E. I., & Cavieres, L. A. (2006). Ecosystem engineering across ecosystems: Do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography*, *33*, 304–313. https://doi.org/10.1111/j.1365-2699.2005.01384.x

Bahr, L. M., & Lanier, W. P. (1981). *The ecology of intertidal oyster reefs of the South Atlantic ocast: A community profile*. U.S. Fish and Wildlife Service, Office of Biological Services.

Barbier, E. B., Hacker, S. D., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). Estuarine and coastal ecosystems and their services. In *Treatise on Estuarine and Coastal Science, Vol 12: Ecological economics of estuaries and coasts* (pp. 109–127). Elsevier Academic Press.

Barrett-Lennard, E. G. (2002). Restoration of saline land through revegetation. *Agricultural Water Management*, *53*, 213–226. https://doi.org/10.1016/S0378-3774(01)00166-4

Berke, S. K. (2010). Functional groups of ecosystem engineers: A proposed classification with comments on current issues. *Integrative and Comparative Biology*, *50*, 147–157. https://doi.org/10.1093/icb/icq077

Berke, S. K. (2012). Biogeographic variability in ecosystem engineering: Patterns in the abundance and behavior of the tube-building polychaete *Diopatra cuprea*. *Marine Ecology Progress Series*, *447*, 1–13. https://doi.org/10.3354/meps09568

Berkenbusch, K., & Rowden, A. A. (2003). Ecosystem engineering–moving away from 'just-so' stories. *New Zealand Journal of Ecology*, *27*, 67–73.

Bishop, M. J., Byers, J. E., Marcek, B. J., & Gribben, P. E. (2012). Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. *Ecology*, *93*, 1388–1401. https://doi.org/10.1890/10-2296.1

Bishop, M. J., Morgan, T., Coleman, M. A., Kelaher, B. P., Hardstaff, L. K., & Evenden, R. W. (2009). Facilitation of molluscan assemblages in mangroves by the fucalean alga *Hormosira banksii*. *Marine Ecology Progress Series*, *392*, 111–122. https://doi.org/10.3354/meps08247

Boogert, N. J., Paterson, D. M., & Laland, K. N. (2006). The implications of niche construction and ecosystem engineering for conservation biology. *Bioscience*, *56*, 570–578.

Breitburg, D. L., Palmer, M. A., & Loher, T. (1995). Larval distributions and the spatial patterns of settlement of an oyster reef fish: Responses to flow and structure. *Marine Ecology Progress Series*, *125*, 45–60. https://doi.org/10.3354/meps125045

Byers, J. E. (2002). Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos*, *97*(3), 449–458. https://doi.org/10.1034/j.1600-0706.2002.970316.x

Byers, J. E. (2009). Invasive animals in marshes: Biological agents of change. In B. Silliman, E. Grosholz, & M. Bertness (Eds.), *Human impacts on salt marshes: A global perspective* (pp. 41–56). University of California Press.

Byers, J. E., Cuddington, K., Jones, C. G., Talley, T. S., Hastings, A., Lambrinos, J. G., Crooks, J., & Wilson, W. (2006). Using ecosystem engineers to restore ecological systems. *Trends in Ecology & Evolution*, *21*, 493–500. https://doi.org/10.1016/j.tree.2006.06.002

Byers, J. E., & Grabowski, J.H. (2014). Soft-sediment communities. In M. D. Bertness, J. F. Bruno, B. R. Silliman & J. J. Stachowicz (Eds.), *Marine community ecology* (pp. 227–249). Sinauer.

Byers, J. E., Grabowski, J. H., Piehler, M. F., Hughes, A. R., Weiskel, H. W., Malek, J. C., & Kimbro, D. L. (2015). Geographic variation in intertidal oyster reef properties and the influence of tidal prism. *Limnology and Oceanography*, *60*, 1051–1063. https://doi.org/10.1002/lno.10073

Byers, J. E., Gribben, P. E., Yeager, C., & Sotka, E. E. (2012). Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. *Biological Invasions*, *14*, 2587–2600. https://doi.org/10.1007/s10530-012-0254-5

Byers, J. E., & Pringle, J. M. (2006). Going against the flow: Retention, range limits and invasions in advective environments. *Marine Ecology Progress Series*, *313*, 27–41. https://doi.org/10.3354/meps313027

Byers, J. E., & Sotka, E. E. (2019). Promoting invasive species to enhance multifunctionality in a native ecosystem still requires strong(er) scrutiny. *Biological Invasions*, *21*, 277–280. https://doi.org/10.1007/s10530-018-1851-8

Byers, J. E., Wright, J. T., & Gribben, P. E. (2010). Variable direct and indirect effects of a habitat-modifying invasive species on mortality of native fauna. *Ecology*, *91*, 1787–1798. https://doi.org/10.1890/09-0712.1

Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., Cardinale, B. J., Hooper, D. U., Dee, L. E., & Duffy, J. E. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, *5*, 111–124. https://doi.org/10.1111/2041-210x.12143

Capelle, J. J., Leuchter, L., de Wit, M., Hartog, E., & Bouma, T. J. (2019). Creating a window of opportunity for establishing ecosystem engineers by adding substratum: A case study on mussels. *Ecosphere*, *10*, e02688. https://doi.org/10.1002/ecs2.2688

Cavaleri, M. A., Ostertag, R., Cordell, S., & Sack, L. (2014). Native trees show conservative water use relative to invasive trees: Results from a removal experiment in a Hawaiian wet forest. *Conservation Physiology*, *2*, cou016. https://doi.org/10.1093/conphys/cou016

Chapman, M. G., & Underwood, A. J. (2011). Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. *Journal of Experimental Marine Biology and Ecology*, *400*, 302–313. https://doi.org/10.1016/j.jembe.2011.02.025

Cleugh, H. A. (1998). Effects of windbreaks on airflow, microclimates and crop yields. *Agroforestry Systems*, *41*, 55–84. https://doi.org/10.1023/A:1006019805109

Coggan, N. V., Hayward, M. W., & Gibb, H. (2018). A global database and 'state of the field' review of research into ecosystem engineering by land animals. *The Journal of Animal Ecology*, *87*, 974–994. https://doi.org/10.1111/1365-2656.12819

Crain, C. M., & Bertness, M. D. (2006). Ecosystem engineering across environmental gradients: Implications for conservation and management. *Bioscience*, *56*, 211–218.

Crooks, J. A. (1998). Habitat alteration and community-level effects of an exotic mussel, Musculista senhousia. *Marine Ecology Progress Series*, *162*, 137–152. https://doi.org/10.3354/meps162137

Crooks, J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos*, *97*, 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Crooks, J. A., & Khim, H. S. (1999). Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology*, *240*, 53–75. https://doi.org/10.1016/S0022-0981(99)00041-6

Cuddington, K., Wilson, W. G., & Hastings, A. (2009). Ecosystem engineers: Feedback and population dynamics. *The American Naturalist*, *173*, 488–498. https://doi.org/10.1086/597216

Cui, W. H., Liu, J. G., Jia, J. L., & Wang, P. F. (2021). Terrestrial ecological restoration in China: Identifying advances and gaps. *Environmental Sciences Europe*, *33*, 123. https://doi.org/10.1186/s12302-021-00563-2

Currin, C. A., Newell, S. Y., & Paerl, H. W. (1995). The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: Considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series*, *121*, 99–116. https://doi.org/10.3354/meps121099

Derksen-Hooijberg, M., Angelini, C., Lamers, L. P. M., Borst, A., Smolders, A., Hoogveld, J. R. H., de Paoli, H., van de Koppel, J., Silliman, B. R., & van der Heide, T. (2018). Mutualistic interactions amplify saltmarsh restoration success. *Journal of Applied Ecology*, *55*, 405–414. https://doi.org/10.1111/1365-2664.12960

Dugan, J. E., Emery, K. A., Alber, M., Alexander, C. R., Byers, J. E., Gehman, A. M., McLenaghan, N. A., & Sojka, S. (2018). Generalizing ecological effects of shoreline armoring across soft sediment environments. *Estuar Coast*, *41*, S180–S196. https://doi.org/10.1007/s12237-017-0254-x

Eldridge, D. J., Whitford, W. G., & Duval, B. D. (2009). Animal disturbances promote shrub maintenance in a desertified grassland. *Journal of Ecology*, *97*, 1302–1310. https://doi.org/10.1111/j.1365-2745.2009.01558.x

Eldridge, D. J., Zaady, E., & Shachak, M. (2002). Microphytic crusts, shrub patches and water harvesting in the Negev Desert: The Shikim system. *Landscape Ecology*, *17*, 587–597. https://doi.org/10.1023/A:1021575503284

Emery, S. M., & Rudgers, J. A. (2014). Biotic and abiotic predictors of ecosystem engineering traits of the dune building grass, *Ammophila breviligulata*. *Ecosphere*, *5*, 87. https://doi.org/10.1890/Es13-00331.1

Emery-Butcher, H. E., Beatty, S. J., & Robson, B. J. (2020). The impacts of invasive ecosystem engineers in freshwaters: A review. *Freshwater Biology*, *65*, 999–1015. https://doi.org/10.1111/fwb.13479

Forseth, I. N., & Innis, A. F. (2004). Kudzu (*Pueraria montana*): History, physiology, and ecology combine to make a major ecosystem threat. *Critical Reviews in Plant Sciences*, *23*, 401–413. https://doi.org/10.1080/07352680490505150

Gagnon, K., Rinde, E., Bengil, E. G. T., Carugati, L., Christianen, M. J. A., Danovaro, R., Gambi, C., Govers, L. L., Kipson, S., Meysick, L., Pajusalu, L., Tüney-Kizilkaya, İ., van de Koppel, J., van der Heide, T., van Katwijk, M. M., & Boström, C. (2020). Facilitating foundation species: The potential for plant-bivalve interactions to improve habitat restoration success. *Journal of Applied Ecology*, *57*, 1161–1179. https://doi.org/10.1111/1365-2664.13605

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Fröberg, M., Stendahl, J., Philipson, C. D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., & Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, *4*, 1340. https://doi.org/10.1038/ncomms2328

Geraldi, N. R., Powers, S. P., Heck, K. L., & Cebrian, J. (2009). Can habitat restoration be redundant? Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks. *Marine Ecology Progress Series*, *389*, 171–180. https://doi.org/10.3354/meps08224

Grabowski, J. H., Brumbaugh, R. D., Conrad, R. F., Keeler, A. G., Opaluch, J. J., Peterson, C. H., Piehler, M. F., Powers, S. P., & Smyth, A. R. (2012). Economic valuation of ecosystem services provided by oyster reefs. *Bioscience*, *62*, 900–909. https://doi.org/10.1525/bio.2012.62.10.10

Grabowski, J. H., Gouhier, T. C., Byers, J. E., Dodd, L. F., Hughes, A. R., Piehler, M. F., & Kimbro, D. L. (2020). Regional environmental variation and local species interactions influence biogeographic structure on oyster reefs. *Ecology*, *101*, e02921. https://doi.org/10.1002/ecy.2921

Grabowski, J. H., & Peterson, C. H. (2007). Restoring oyster reefs to recover ecosystem services. In K. Cuddington, J. E. Byers, W. Wilson, & A. Hastings (Eds.), *Ecosystem Engineering: Plants to protists* (pp. 281–298). Elsevier Academic Press.

Gray, J. S. (1974). Animal-sediment relationships. *Oceanography Marine Biology Annual Review*, *12*, 223–261.

Gribben, P. E., Angelini, C., Altieri, A. H., Bishop, M. J., Thomsen, M. S., & Bulleri, F. (2019). Facilitation cascades in marine ecosystems: A synthesis and future directions. *Oceanography Marine Biology*, *57*, 127–168. https://doi.org/10.1201/9780429026379

Guiden, P. W., Barber, N. A., Blackburn, R., Farrell, A., Fliginger, J., Hosler, S. C., King, R. B., Nelson, M., Rowland, E. G., Savage, K., Vanek, J. P., & Jones, H. P. (2021). Effects of management outweigh effects of plant diversity on restored animal communities in tallgrass prairies. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2015421118. https://doi.org/10.1073/pnas.2015421118

Gutierrez, J. L., Jones, C. G., Byers, J. E., Arkema, K. K., Berkenbusch, K., Commito, J. A., Duarte, C. M., Hacker, S. D., Lambrinos, J. G., Hendriks, I. E., Hogarth, P. J., Palomo, M. G., & Wild, C. (2011). Physical Ecosystem Engineers and the Functioning of Estuaries and Coasts. In *Treatise on Estuarine and Coastal Science*, *Vol 7: Functioning of ecosystems at the land–ocean interface* (pp. 53–81). Elsevier Acadmic Press.

Guy-Haim, T., Lyons, D. A., Kotta, J., Ojaveer, H., Queiros, A. M., Chatzinikolaou, E., Arvanitidis, C., Como, S., Magni, P., Blight, A. J., Orav-Kotta, H., Somerfield, P. J., Crowe, T. P., & Rilov, G. (2018). Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: A global review and meta-analysis. *Global Change Biology*, *24*, 906–924. https://doi.org/10.1111/gcb.14007

Hacker, S. D., Zarnetske, P., Seabloom, E., Ruggiero, P., Mull, J., Gerrity, S., & Jones, C. (2012). Subtle differences in two non-native congeneric beach grasses significantly affect their colonization, spread, and impact. *Oikos*, *121*, 138–148. https://doi.org/10.1111/j.1600-0706.2011.18887.x

Haram, L. E., Kinney, K. A., Sotka, E. E., & Byers, J. E. (2018). Mixed effects of an introduced ecosystem engineer on the foraging behavior and habitat selection of predators. *Ecology*, *99*, 2751–2762. https://doi.org/10.1002/ecy.2495

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S., & Wilson, W. G. (2007). Ecosystem engineering in space and time. *Ecology Letters*, *10*, 153–164. https://doi.org/10.1111/j.1461-0248.2006.00997.x

Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, *110*, 449–460. https://doi.org/10.1007/s004420050180

Jones, C. G., Gutierrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G., & Talley, T. S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, *119*, 1862–1869. https://doi.org/10.1111/j.1600-0706.2010.18782.x

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, *69*, 373–386. https://doi.org/10.2307/3545850

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, *78*, 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:Paneoo]2.0.Co;2

Kidwell, S. M. (1986). Taphonomic feedback in miocene assemblages: Testing the role of dead hardparts in benthic communities. *PALAIOS*, *1*, 239–255.

Koch, E. W., Barbier, E. B., Silliman, B. R., Reed, D. J., Perillo, G. M. E., Hacker, S. D., Granek, E. F., Primavera, J. H., Muthiga, N., Polasky, S., Halpern, B. S., Kennedy, C. J., Kappel, C. V., & Wolanski, E. (2009). Non-linearity in ecosystem services: Temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment*, *7*, 29–37. https://doi.org/10.1890/080126

Kollars, N. M., Byers, J. E., & Sotka, E. E. (2016). Invasive decor: An association between a native decorator worm and a non-native seaweed can be mutualistic. *Marine Ecology Progress Series*, *545*, 135–145. https://doi.org/10.3354/meps11602

Komyakova, V., Jones, G. P., & Monday, P. L. (2018). Strong effects of coral species on the diversity and structure of reef fish communities: A multi-scale analysis. *PLoS ONE*, *13*, e0202206. https://doi.org/10.1371/journal.pone.0202206

Koutika, L.-S., Zagatto, M. R. G., Pereira, A. P.d. A., Miyittah, M., Tabacchioni, S., Bevivino, A., & Rumpel, C. (2021). Does the introduction of N_2-fixing trees in forest plantations on tropical soils ameliorate low fertility and enhance carbon sequestration via interactions between biota and nutrient availability? Case studies from Central Africa and South America. *Frontiers in Soil Science*, *1*, 752747. https://doi.org/10.3389/fsoil.2021.752747

Lenihan, H. S. (1999). Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. *Ecological Monographs*, *69*, 251–275. https://doi.org/10.2307/2657157

Lenihan, H. S., & Peterson, C. H. (1998). How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecological Applications*, *8*, 128–140. https://doi.org/10.1890/1051-0761(1998)008[0128:Hhdtfd]2.0.Co;2

Lenihan, H. S., Peterson, C. H., Byers, J. E., Grabowski, J. H., Thayer, G. W., & Colby, D. R. (2001). Cascading of habitat degradation: Oyster reefs invaded by refugee fishes escaping stress. *Ecological Applications*, *11*, 764–782. https://doi.org/10.2307/3061115

Leuzinger, S., & Rewald, B. (2021). The who or the how? Species vs. ecosystem function priorities in conservation ecology. *Front. Plant Science*, *12*, 758413. https://doi.org/10.3389/fpls.2021.758413

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F. T., Mace, G., Whittingham, M. J., & Fischer, M. (2018). Redefining ecosystem multifunctionality. *Nature Ecology & Evolution*, *2*, 427–436. https://doi.org/10.1038/s41559-017-0461-7

Menge, B. A., & Sutherland, J. P. (1987). Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, *130*, 730–757. https://doi.org/10.1086/284741

Meyer, D. L., Townsend, E. C., & Thayer, G. W. (1997). Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restoration Ecology*, *5*, 93–99. https://doi.org/10.1046/j.1526-100X.1997.09710.x

Moore, J. M., & Picker, M. D. (1991). Heuweltjies (earth mounds) in the Clanwilliam District, Cape Province, South Africa: 4000-year-old termite nests. *Oecologia*, *86*, 424–432. https://doi.org/10.1007/Bf00317612

Moore, J. W. (2006). Animal ecosystem engineers in streams. *Bioscience*, *56*, 237–246. https://doi.org/10.1641/0006-3568(2006)056[0237:Aeeis]2.0.Co;2

Morris, R. L., Bilkovic, D. M., Boswell, M. K., Bushek, D., Cebrian, J., Goff, J., Kibler, K. M., La Peyre, M. K., McClenachan, G., Moody, J., Sacks, P., Shinn, J. P., Sparks, E. L., Temple, N. A., Walters, L. J., Webb, B. M., & Swearer, S. E. (2019). The application of oyster reefs in shoreline protection: Are we over-engineering for an ecosystem engineer? *Journal of Applied Ecology*, *56*, 1703–1711. https://doi.org/10.1111/1365-2664.13390

Myers, A. C. (1972). Tube-worm-sediment relationships of *Diopatra cuprea* (Polychaeta-Onuphidae). *Marine Biology*, *17*, 350–356. https://doi.org/10.1007/Bf00366746

Newell, R. I. E. (2004). Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: A review. *Journal of Shellfish Research*, *23*, 51–61.

Palmer, M. A., Ambrose, R. F., & Poff, N. L. (1997). Ecological theory and community restoration ecology. *Restoration Ecology*, *5*, 291–300. https://doi.org/10.1046/j.1526-100X.1997.00543.x

Pannell, D. J., & Ewing, M. A. (2006). Managing secondary dryland salinity: Options and challenges. *Agr Water Manage*, *80*, 41–56. https://doi.org/10.1016/j.agwat.2005.07.003

Peterson, C. H., Grabowski, J. H., & Powers, S. P. (2003). Estimated enhancement of fish production resulting from restoring oyster reef habitat: Quantitative valuation. *Marine Ecology Progress Series*, *264*, 249–264. https://doi.org/10.3354/meps264249

Piehler, M. F., & Smyth, A. R. (2011). Habitat-specific distinctions in estuarine denitrification affect both ecosystem function and services. *Ecosphere*, *2*, 12. https://doi.org/10.1890/Es10-00082.1

Reise, K. (2002). Sediment mediated species interactions in coastal waters. *Journal of Sea Research*, *48*, 127–141. https://doi.org/10.1016/S1385-1101(02)00150-8

Rilov, G., Mant, R., Lyons, D., Bulleri, F., Benedetti-Cecchi, L., Kotta, J., Queiros, A. M., Chatzinikolaou, E., Crowe, T., & Guy-Haim, T. (2012). How strong is the effect of invasive ecosystem engineers on the distribution patterns of local species, the local and regional biodiversity and ecosystem functions? *Estuarine, Coastal and Shelf Science*, *1*, 10. https://doi.org/10.1186/2047-2382-1-10

Romero, G. Q., Goncalves-Souza, T., Vieira, C., & Koricheva, J. (2015). Ecosystem engineering effects on species diversity across ecosystems: A meta-analysis. *Biological Reviews*, *90*, 877–890. https://doi.org/10.1111/brv.12138

Rosenberg, R., Nilsson, H. C., & Diaz, R. J. (2001). Response of benthic fauna and changing sediment redox profiles over a hypoxic gradient. *Estuarine, Coastal and Shelf Science*, *53*, 343–350. https://doi.org/10.1006/ecss.2001.0810

Ruesink, J. L., Lenihan, H. S., Trimble, A. C., Heiman, K. W., Micheli, F., Byers, J. E., & Kay, M. C. (2005). Introduction of non-native oysters: Ecosystem effects and restoration implications. *Annual Review of Ecology, Evolution, and Systematics*, *36*, 643–689. https://doi.org/10.1146/annurev.ecolsys.36.102003.152638

Schlaepfer, M. A., Sax, D. F., & Olden, J. D. (2011). The potential conservation value of non-native species. *Conservation Biology*, *25*, 428–437. https://doi.org/10.1111/j.1523-1739.2010.01646.x

Shachak, M., Pickett, S. T. A., Boeken, B., & Zaady, E. (1999). Managing patchiness, ecological flows, productivity, and diversity in drylands: Concepts and applications in the Negev Desert. In T. W. Hoekstra & M. Shachak (Eds.), *Arid lands management: Toward ecological sustainability* (pp. 254–263). University of Illinois Press.

Shachak, M., Sachs, M., & Moshe, I. (1998). Ecosystem management of desertified shrublands in Israel. *Ecosystems*, *1*, 475–483. https://doi.org/10.1007/s100219900043

Schutte, V. G. M., & Byers, J. E. (2017). Variation in a simple trait of mangrove roots governs predator access to, and assemblage composition of, epibiotic sponges. *Marine Ecology Progress Series*, *573*, 15–23. https://doi.org/10.3354/meps12160

Silliman, B. R., Schrack, E., He, Q., Cope, R., Santoni, A., van der Heide, T., Jacobi, R., Jacobi, M., & van de Koppel, J. (2015). Facilitation shifts paradigms and can amplify coastal restoration efforts. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 14295–14300. https://doi.org/10.1073/pnas.1515297112

Smith, R. S., Blaze, J. A., & Byers, J. E. (2021). Dead litter of resident species first facilitates and then inhibits sequential life stages of range-expanding species. *Journal of Ecology*, *109*, 1649–1664. https://doi.org/10.1111/1365-2745.13586

Smith, R. S., Blaze, J. A., Osborne, T. Z., & Byers, J. E. (2018). Facilitating your replacement? Ecosystem engineer legacy affects establishment success of an expanding competitor. *Oecologia*, *188*, 251–262. https://doi.org/10.1007/s00442-018-4184-5

Smyth, A. R., Geraldi, N. R., Thompson, S. P., & Piehler, M. F. (2016). Biological activity exceeds biogenic structure in influencing sediment nitrogen cycling in experimental oyster reefs. *Marine Ecology Progress Series*, *560*, 173–183. https://doi.org/10.3354/meps11922

Sotka, E. E., & Byers, J. E. (2019). Not so fast: Promoting invasive species to enhance multifunctionality in a native ecosystem requires strong(er) scrutiny. *Biological Invasions*, *21*, 19–25. https://doi.org/10.1007/s10530-018-1822-0

Sousa, R., Gutierrez, J. L., & Aldridge, D. C. (2009). Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions*, *11*, 2367–2385. https://doi.org/10.1007/s10530-009-9422-7

Stachowicz, J. J., Fried, H., Osman, R. W., & Whitlatch, R. B. (2002). Biodiversity, invasion resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology*, *83*, 2575–2590.

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, *19*, 46–53. https://doi.org/10.1016/j.tree.2003.10.005

Tait, L. W., Lohrer, A. M., Townsend, M., Atalah, J., Floerl, O., & Inglis, G. J. (2020). Invasive ecosystem engineers threaten benthic nitrogen cycling by altering native infaunal and biofouling communities. *Scientific Reports*, *10*, 1–11. https://doi.org/10.1038/s41598-020-58557-8

Thomsen, M. S., & McGlathery, K. (2005). Facilitation of macroalgae by the sedimentary tube forming polychaete *Diopatra cuprea*. *Estuarine, Coastal and Shelf Science*, *62*, 63–73. https://doi.org/10.1016/j.ecss.2004.08.007

Thomsen, M. S., Wernberg, T., Altieri, A. H., Tuya, F., Gulbransen, D., McGlathery, K. J., Holmer, M., & Silliman, B. R. (2010). Habitat cascades: The conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integrative and Comparative Biology*, *50*, 158–175. https://doi.org/10.1093/icb/icq042

Tilman, D., Lehman, C. L., & Thomson, K. T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 1857–1861. https://doi.org/10.1073/pnas.94.5.1857

Tyrrell, M. C., & Byers, J. E. (2007). Do artificial substrates favor nonindigenous fouling species over native species? *Journal of Experimental Marine Biology and Ecology*, *342*, 54–60. https://doi.org/10.1016/j.jembe.2006.10.014

Valiela, I., & Rietsma, C. S. (1995). Disturbance of salt marsh vegetation by wrack mats in Great Sippewissett Marsh. *Oecologia*, *102*, 106–112. https://doi.org/10.1007/Bf00333317

Volkenborn, N., Robertson, D. M., & Reise, K. (2009). Sediment destabilizing and stabilizing bio-engineers on tidal flats: Cascading effects of experimental exclusion. *Helgoland Marine Research*, *63*, 27–35. https://doi.org/10.1007/s10152-008-0140-9

Wasson, K., Fenn, K., & Pearse, J. S. (2005). Habitat differences in marine invasions of central California. *Biological Invasions*, *7*, 935–948. https://doi.org/10.1007/s10530-004-2995-2

Woodin, S. A. (1976). Adult-larval interactions in dense infaunal assemblages - Patterns of abundance. *Journal of Marine Research*, *34*, 25–41.

Woodin, S. A. (1978). Refuges, disturbance, and community structure: Marine soft-bottom example. *Ecology*, *59*, 274–284. https://doi.org/10.2307/1936373

Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, *132*, 96–101. https://doi.org/10.1007/s00442-002-0929-1

Wright, J. T., Byers, J. E., DeVore, J. L., & Sotka, E. E. (2014). Engineering or food? mechanisms of facilitation by a habitatforming invasive seaweed. *Ecology*, *95*, 2699–2706. https://doi.org/10.1890/14-0127.1

Yeakel, J. D., Pires, M. M., de Aguiar, M. A. M., O'Donnell, J. L., Guimaraes, P. R., Gravel, D., & Gross, T. (2020). Diverse interactions and ecosystem engineering can stabilize community assembly. *Nature Communications*, *11*, 3307. https://doi.org/10.1038/s41467-020-17164-x

Zahra, S., Novotny, V., & Fayle, T. M. (2021). Do reverse Janzen-Connell effects reduce species diversity? *Trends in Ecology & Evolution*, *36*, 387–390. https://doi.org/10.1016/j.tree.2021.02.002

Zarnetske, P. L., Hacker, S. D., Seabloom, E. W., Ruggiero, P., Killian, J. R., Maddux, T. B., & Cox, D. (2012). Biophysical feedback mediates effects of invasive grasses on coastal dune shape. *Ecology*, *93*, 1439–1450. https://doi.org/10.1890/11-1112.1

Zavaleta, E. S., Pasari, J. R., Hulvey, K. B., & Tilman, G. D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 1443–1446. https://doi.org/10.1073/pnas.0906829107

How to cite this article: Byers, J. E. (2024). Using ecosystem engineers to enhance multiple ecosystem processes. *Functional Ecology*, *38*, 22–36. https://doi.org/10.1111/1365-2435.14130