The ghosts of ecosystem engineers: Legacy effects of biogenic modifications

Lindsey K. Albertson, Leonard S. Sklar, Benjamin B. Tumolo, Wyatt F. Cross, Scott F. Collins, H. Arthur Woods

This is the peer reviewed version of the following article: [The ghosts of ecosystem engineers: Legacy effects of biogenic modifications. Functional Ecology 38, 1 p52-72 (2022)], which has been published in final form at https://doi.org/10.1111/1365-2435.14222. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions: https://authorservices.wiley.com/author-resources/Journal-Authors/licensing/self-archiving.html#3.

The ghosts of ecosystem engineers: Legacy effects of biogenic modifications

Lindsey K. Albertson[1ɫ], Leonard S. Sklar[2], Benjamin B. Tumolo[1], Wyatt F. Cross[1], Scott F. Collins[3], and H. Arthur Woods[4]

Author affiliations

[1]Department of Ecology, Montana State University, USA

[2]School of Environmental Science, Simon Fraser University, Canada

[3]Department of Natural Resources Management, Texas Tech University, USA

[4]Division of Biological Sciences, University of Montana, USA

[ɫ]corresponding author: Lindsey Albertson; lindsey.albertson@montana.edu

Running headline: Legacy effects of ecosystem engineers

Acknowledgements

We thank Dr. M. Daniels, S. Fritz, and Dr. E. Scholl for helpful discussion of the study topic. Funding was provided, in part, by the National Science Foundation (DEB 1556684, 1556487, and 1945941), Montana State University, and Texas Tech University.

Conflict of interest statement: None of the authors has a conflict to declare.

Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.w6m905qss (Albertson et al. 2022).

Author contributions

LKA conceived the idea; All authors designed the research; LKA and BBT collected the data; LKA led the writing of the manuscript; All authors contributed significantly to the writing, critically evaluated the drafts, and gave final approval for publication.

Abstract

1. Ecosystem engineers strongly influence the communities in which they live by modifying habitats and altering resource availability. These biogenic changes can persist beyond the presence of the engineer, and such modifications are known as ecosystem engineering legacy effects.
2. Although many authors recognize ecosystem engineering legacies, and some case studies quantify the effects of legacies, few general frameworks describe their causes and consequences across species or ecosystem types.
3. Here, we synthesize evidence for ecosystem engineering legacies and describe how consideration of key traits of engineers improves understanding of which engineers are likely to leave persistent biogenic modifications .
4. Our review demonstrates that engineering legacies are ubiquitous, with substantial effects on individuals, communities, and ecosystem processes. Attributes that may promote the persistence of influential legacies relate to an engineer's traits, including its body size, lifespan, and living strategy (individual, conspecific group, or collection of multiple co-occurring species).
5. Additional lines of inquiry, such as how the recipients respond (e.g., density or richness) or the mechanism of engineering (e.g., burrowing or structure building), should be included in future ecosystem engineering legacy research.
6. Understanding patterns of these persistent effects of ecosystem engineers and evaluating the consequences of losing them is an important area of research needed for understanding long-term ecological responses to global change and biodiversity loss.

Keywords: abandoned, habitat, persistence, resource, temporal, traits

1. Introduction

Legacies are ideas, objects, or processes that originate in the past and persist into and influence the future. Legacies sometimes arise from extraordinary actions that can change the course of history as well as expectations for what is possible (Miller et al., 2009; Wittenberg, 2013; Wohl, 2019). For example, most people are familiar with the legacy of Michael Jordan, who redefined what is possible in basketball. In nature, we also recognize legacies, such as those left by abiotic events like hurricanes, heat waves, earthquakes, and retreat of glaciers, which can have striking and persistent effects on physical and chemical conditions long after these events have ceased (Connell, 1978; Dunson & Travis, 1991; Hughes et al., 2019). In addition, anthropogenic activities such as nutrient pollution and mining leave well-recognized contaminant legacies that continue to influence water quality over many decades (Basu et al., 2022; Lima et al., 2016). Less appreciated, however, are the legacies left by the myriad organisms that influence the availability and character of habitat and resources in ecosystems (Cuddington, 2011).

Ecosystem engineers are organisms that alter the abiotic environment, producing changes to habitat and resource supply that govern community assembly, ecosystem processes, and niche construction (Table 1; Gutiérrez & Jones, 2006; Jones et al., 1994; Wright & Jones, 2006). Modifications can arise from activities of individuals, groups of conspecifics, and assemblages of co-occurring organisms, and they often last longer than the organisms themselves. Such modifications are known as ecosystem engineering legacies (Table 1; Cuddington, 2011; Hastings et al., 2007). Our definition of an ecosystem engineer extends the classical definition

(Jones et al. 1994) by including organisms that modify the environment in any of the following ways: the presence of their own bodies (autogenic; e.g, corals); activities that transform the state of local materials or chemicals and often result in an extended phenotype (Table 1; allogenic; e.g., nest building); and simultaneous physical, other non-consumptive, and trophic modification (e.g., salmon disturbing riverbed sediment and organic matter; Prugh & Brashares, 2012; Rex et al., 2014; Wilby et al., 2001). Despite the substantial – and often long-lasting – influence of biota on the environment, appreciation of ecosystem engineering legacies as a significant factor shaping the structure and function of Earth's ecosystems has been relatively slow to develop (Dietrich & Perron, 2006; Naylor et al., 2002; Rice, 2021). In addition, frameworks that identify the general traits of engineers that are likely to leave legacies are still scarce (Frauendorf et al., 2021; Hastings et al. 2007).

Because ecosystem engineering effects are widespread, it is increasingly important that legacies are included in understanding maintenance of ecosystems and in predicting the biotic outcomes of anthropogenic change more broadly (Estes & Vermeij, 2022; Frauendorf et al., 2021). Here, we review the evidence for ecosystem engineering legacies in nature using four approaches. First, we set the stage by describing select case studies of legacies in the literature and the trajectory of ecosystem engineering legacy knowledge. Second, we use a conceptual framework designed around underlying organismal phenotypes to compare legacies across different engineering taxa. Third, we use a synthesis to demonstrate how the conceptual framework applies to published legacy examples. And finally, we discuss directions for continued development of metrics that will advance understanding of ecosystem engineering legacies and the roles that organisms play in influencing the structure and function of communities and ecosystems.

2. Review of ecosystem engineering legacies

2.1 Examples of ecosystem engineering legacies

Legacies may last for milliseconds to millennia and their spatial footprint can be small or large. For instance, crawling slugs (ca. 2 cm length) leave behind mucous residues that provide a surface and resources for microbial colonists (Table 2; Theenhaus & Scheu, 1996) that is relatively small and persists for a short period of time. Other legacies are especially large and long-lasting, with the potential to influence the system long after the engineer is gone (Table 2). For example, monitor lizards (ca. 1.5 m length) construct burrows that are used by amphibians and arthropods (Doody et al., 2021); individual spawning salmon disturb riverbeds at small spatial and temporal scales (Collins et al., 2011) yet the collective effects of salmon populations and spawning behavior on riverbed geomorphology have broad consequences for watershed evolution (Fremier et al., 2018). Casts from bioturbating worms in marine tidal flats leave behind evidence that is visible in the sedimentary record over geologic time (Cribb & Bottjer, 2020; Kristensen et al., 2012). In addition, microbial communities in marine environments that formed stromatolites fostered the rise of different chemical pathways over evolutionary time (Altermann, 2008; Paterson et al., 2008), and photosynthetic organisms associated with these features created the atmosphere on which we and all aerobic organisms depend (Blankenship, 2010). Together, these select examples illustrate the potential for many different organisms to participate in ecosystem engineering legacies over a very wide range of temporal and spatial scales.

2.2 Fundamental attributes of biogenic modifications

Attributes that are often used to determine the magnitudes of ecological legacies, including ecosystem engineering legacies, are duration, spatial extent, and frequency through time and space (Figure 1). The magnitude of a physical drought legacy in a forest, for example, can depend on a suite of attributes, including the duration, spatial location, and timing of the current drought, as well as the time elapsed (1/temporal frequency) since other recent droughts (Kannenberg et al., 2020). Along with duration and spatial extent, frequency in space is especially salient for ecosystem engineering legacies. Consider soil dwelling organisms, which can have engineering effects on soil properties and on communities of arthropods and plants. Many ants, for example, construct below-ground nests, into which colonies introduce terrestrial organic matter (e.g., leaf-fungus farmed by leaf-cutting ants; Schoenian et al., 2011). High densities of nests may transform soil properties over large spatial scales, even though each individual nest affects a limited area. Likewise for earthworms – although individual worms have limited capacity to alter soils, large populations can have profound effects on soil properties across large areas, with wide ranging effects on other soil arthropods and local plant communities (Eisenhauer, 2010; Holdsworth et al., 2007).

Like those that are frequent in space, legacies that are frequent in time will often be more important than those that occur rarely. For example, the ability of marine invertebrates to move, as well as to obtain nutrients and gases from their environment, is influenced by the persistent presence of surface-fouling ecosystem engineers growing on the invertebrate itself. Sea spiders (pycnogonids) obtain oxygen from seawater via pores in their cuticles (Lane et al., 2018), but oxygen availability can be blocked by surface fouling organisms. Some kinds of fouling, like biofilms, are ubiquitous and the invertebrate must contend with their growth and subsequent respiratory effects on a daily basis by spending a substantial proportion of their time grooming their surfaces with specialized appendages. Other kinds of fouling, like colonies of bryozoans or large barnacles, could have large effects but they occur much less frequently than do biofilms (Lane et al., 2016). So, the consistently present biofilms are more likely to matter to the sea spider's biogeochemical environment than are rarely present bryozoans or barnacles.

Temporal frequency and spatial extent may be directly or indirectly related to one another. Whales for example, often fall after death to the ocean floor, where their carcasses engineer the local environment by supporting diverse communities of other organisms that occupy and feed on them (Roman et al. 2014; Smith et al., 2015). In this context, 'spatial extent' refers to the body size of the dead whale. Larger carcasses probably occur less frequently than do small ones because not as many individuals survive to later life stages, but they nevertheless can leave large-magnitude legacies by persisting for long periods of time (sometimes decades to centuries; Smith et al., 2015).

2.3 Legacy in the eye of the beholder

A component of a legacy's importance depends on the impact it has on recipient individuals, species, and biological processes, as well as environmental context. In some instances, legacies affect one or a few individuals, without broader effects on populations, communities, or ecosystems (Farji-Brener & Werenkraut, 2015). These legacies may be considered less influential. However, if those single or few individuals belong to an endemic, endangered, or keystone species, then the impact of that legacy is amplified. Beyond ways in which legacies affect individuals, ecosystem engineering activities that modify habitat or resources in ways that propagate to the community- or ecosystem-level could leave particularly impactful legacies.

2.3.1 Community level responses

Multiple, co-occurring engineering species can create collective legacies (Caliman et al., 2013; Thomsen et al., 2018; see section 3.3). For example, trees modify habitats that foster epiphytes, and these epiphytes also provide habitat to other organisms (Thomsen et al., 2010). Such effects often can persist even when the engineers are no longer living, but generally to a lesser extent than when they are alive (Bologna & Heck, 1999). Collective legacies also manifest at the community level when multiple species are influenced by and respond to the legacy. As a result, a legacy that affects one recipient may be considered less important than one that affects a diverse suite of species or a whole community (Thomsen et al., 2018). For example, a large number (up to 28) of different species of springtail (Collembola) can live in soil patches created by mobile earthworms (Lavelle, 2002; Loranger et al., 1998). Sometimes the recipient taxa are ecosystem engineers themselves (i.e., a ‘facilitation cascade’), whereby the presence of one engineer promotes the presence of others even after that original engineer is gone (Thomsen et al., 2010), an idea that parallels the conceptual framework of succession and replacement of species as the environment is altered by the previous occupants (Drury & Nisbet, 1973; Odum, 1969). Finally, some engineers may leave legacies that could extend across ecosystem boundaries. For instance, freshwater mussels increase the productivity of emergent aquatic plants by increasing water-column phosphorous, and the plants in turn attract and provide resources for terrestrial herbivores (Lopez et al., 2020). Because mussel shells continue to affect the environment after the mussels are dead, this cross-boundary effect may persist through time.

2.3.2 Ecosystem level responses

Besides influencing communities, legacies can also generate persistent effects on ecosystem and biogeochemical processes. These effects are evident when engineering activities have lasting effects on material resources (e.g., nitrogen and carbon) or environmental conditions (e.g., light, temperature, and redox potential; Gutiérrez & Jones, 2006). Nitrogen fixation by many early successional or invasive plant species, for example, can fuel primary production of other taxa long after they are gone (Chapin et al., 1994). Von Holle et al. (2013) found that nitrogen pools remained elevated at least 14 years following the removal of nonnative N_2-fixing black locust trees. Other ecosystem engineers such as beavers or earthworms often reconfigure the amount and structure of river sediments or forest soils for many years following their disappearance (Naiman et al., 1988). In the case of beaver, although many of the engineered changes may be reversed over 5-10 years, some may last much longer (Wohl, 2021). For instance, Laurel and Wohl (2018) found that the effects of beavers on river geomorphology persist for >30 years after the beavers stop maintaining a dam. Their influence on the storage of organic carbon in floodplains – and associated carbon turnover and mineralization (Naiman et al., 1986) – may persist for even longer.

Biogenic legacies can also drive ecological feedbacks that enhance their persistence. This may be particularly evident if legacies change the character of natural or anthropogenic disturbance regimes. In western North America, forest insect outbreaks can have lasting effects on ecosystem properties (e.g., soil moisture, surface fuel accumulation) that may alter susceptibility to future wildfires (Meigs et al., 2016). Such changes have the potential to feed back and influence subsequent insect outbreaks (Bergeron and Leduc, 1998). Grazing by large herbivores, together with fire, can produce and maintain African savannah ecosystems by removing trees and woody vegetation. Grassland conditions persist beyond the lifespan of the herbivores and promote future grazing and fire that reinforces the savannah state (Lenton et al., 2021; Marshall et al., 2018).

2.3.3 Directional responses by the recipients

Ecosystem engineers inevitably create conditions that are better for some organisms or ecological processes than for others; thus legacies can be simultaneously positive or negative (Daleo et al., 2006; Gribben et al., 2013). For example, ecosystem engineering kangaroo rats (*Dipodomys ingens*) create networks of burrows that decrease bird and plant diversity potentially through soil disturbance but increase invertebrate diversity potentially through increased habitat availability or food subsidies (Prugh & Brashares, 2012). Another important avenue by which directionality mediates a legacy occurs when ecosystem engineers alter their surroundings through multiple, co-occurring processes that may leave differing positive or negative effects. Spawning salmon, for example, may beneficially engineer streams by disturbing sediments and enriching nutrients, but they may also detrimentally engineer streams by transporting pollutants (Baker et al., 2009; Gerig et al., 2016). Indeed, decomposing fish tissues may fertilize streams while also leaching persistent organic contaminants, which can bioaccumulate in the tissues of other organisms (Baker et al., 2009; Gerig et al., 2016; Morrissey et al., 2012).

2.3.4 Environmental disturbance

Engineering effects have the greatest potential to leave legacies when the modifications are resistant to environmental disturbances or when these disturbances are rare or small in magnitude (Johnstone et al., 2016). The strength of pairwise interactions between species, such as an engineer and the recipient of the modified environment, is very likely affected by environmental context (Germain et al., 2018). For example, dead animal flesh, bone, and cartilage each provide a resource legacy that attracts scavengers (hours to days) or slowly releases phosphorus (months to years) into soil or water until the animal remains are gone. However, any legacy effect could be negated if those remains are washed away by waves, flooding, or another form of disturbance (Cortés-Avizanda et al., 2012; Laidre & Greggor, 2015).

Although extreme events are by definition rare, they may be large enough in magnitude to erase existing modifications very rapidly. For example, when spawning salmon dig nests, they scour river sediments, enrich biofilms, and dislodge macroinvertebrates in small patches (Collins et al., 2011; Verspoor et al., 2011). Nests can withstand daily stream flows, but spring runoff can disturb sediments and destroy a nest several months later. Thus, engineering effects can be robust to daily fluctuations but destroyed by stronger events. As another example, a beaver can construct a dam in a few months and maintain it for years (Cenderelli, 2000, Johnson-Bice et al., 2022). The dam’s structural integrity, and thus resilience, depends on features such as size and construction material (Woo & Waddington, 1990). Although dams can withstand a range of disturbances for years, intense precipitation, flooding, and collapse of upstream dam(s) – all relatively unpredictable events – can destroy them (Cenderelli, 2000; Rutherford, 1953). In both examples, legacy effects reflect a balance between buildup of the engineered structure and erosion of it by the local disturbance regime. Legacy duration will thus depend strongly on the frequency, extent, and severity of disturbances.

How recipients of the engineering modification perceive or use the legacy also relates to environmental context. In harsh environments with large or frequent disturbances, recipients that use the engineering modification may rely more heavily on the changes imposed by the engineer (Bertness & Callaway, 1994). That is, the positive effect of the modification by the ecosystem engineer will play an increasingly important role in creating suitable habitat or providing valuable resources when an environment is otherwise highly disturbed.

2.4 Traits of the engineer

Another component of a legacy's importance relates to traits of the engineer itself. The population density of an engineer, for example, should modulate the legacy. Earthworms offer a clear example. Individual worms create soil casts that alter soil aggregation and oxygenation at small spatio-temporal scales, equivalent to or less than that of an individual earthworm's own body size and lifetime (Table 2). However, the collective effects of earthworm populations can be realized at macroscales. As earthworms have expanded into northern forests, for example, they have released large amounts of soil carbon through their casts with consequences for ecosystem-level nutrient cycling and greenhouse gas emissions (Table 2; Frelich et al., 2019). Another example of individually minor effects that become significant at high population densities is soil disturbance by mammals. A single wallow made by a bison, for example, may only have a 4-meter diameter and last 25 years, but in places like Yellowstone National Park, where the bison population has grown from 500 individuals in the 1970s to 5,000 today, the cumulative effects of all wallows on the landscape persist for many decades and shape physical, chemical, and biological processes (Nickell et al., 2018).

Behavioral traits can also affect legacies (Gribben et al. 2013). How conspecifics interact with one another is an important behavioral consideration that likely determines legacy magnitude. For example, some species have individuals that are solitary (e.g., a rabbit), while other species have individuals that live in extremely close proximity groups (e.g. mussels). Additionally, some legacies emerge from the combined effects of multiple species (Bétard, 2021). As such, collective legacies can arise from either multiple individuals of the same species acting together to modify the environment or from multiple, coexisting and interacting species, and these often shift the abiotic environment to a new stable state. One example of this type of collective legacy is the formation of soil. For coherent rock to be transformed into a porous matrix of disaggregated minerals and organic material typically requires the joint actions of microorganisms, invertebrates, large plants, and even mammals. The soils that blanket the well-studied mountains of the Luquillo National Forest of Puerto Rico are created in part by bacteria (*Cupriavidus*; Liermann et al., 2015; Napieralski et al., 2019) that oxidize iron-bearing minerals, Tabonuco trees (*Dacryodes excelsa*; Scatena & Lugo, 1995) that root in and break apart rock and contribute some of their own biomass, and worms (*Pontoscolex corethrurus*; Lavelle et al., 2007) that mix soils and leave nutrient-rich castings. None of the species alone creates soil from rock, but each contributes this pervasive alteration of the physical environment.

The step-pool morphology of travertine rivers provides another example of a collective legacy that illustrates how diverse assemblages of organisms can shift the abiotic environment to a new stable state (Fuller et al., 2011). Fallen trees and large-woody debris catalyze travertine dam formation in streams, by causing high velocity overflow that drives $CaCO_3$ precipitation from super-saturated spring-fed baseflow (Viles & Pentecost, 1999). Nascent dams trap floating algal mats and leaf litter, which provide surface area for travertine crystals to precipitate (Compson et al., 2009; Merz-Preis & Riding, 1999), a process enhanced by microbial photosynthesis which raises local pH (Ferris et al., 1995; Pentecost, 2005; Takashima & Kano, 2008).

The temporal magnitude of collective legacies cannot be easily quantified at the scale of the individual species, whose lifespans range from hours (bacteria) to centuries (trees). For soils, travertine, and other collective legacies created by multiple co-occurring engineers, the relevant time-scale would capture how long the effect would persist if all organisms abruptly ceased their work. For long-lived legacies, the potential decay time should scale with the residence time of the bio-mediated material at steady-state. For example, the soils produced by collective ecosystem engineering legacies described previously in the mountain forests of Puerto Rico are in an approximate steady state, in which soil production from rock below is balanced by soil erosion into down-slope river channels. Using representative values of soil depth (~1 m) and soil production and long-term erosion rate (10^{-4} m/yr), a steady-state residence time, and thus potential legacy time scale would be 10,000 years (Willenbring et al., 2013). In other geologic and climatic settings, where soils are both thicker and produced more slowly, residence times can be orders of magnitude longer (Almond et al., 2007).

Another important behavioral consideration is how the engineer carries out the activity that alters habitat or resources. Organisms that alter the environment through their own physical presence (autogenic engineers; e.g., tree stumps) operate differently than organisms that actively transform the environment external to their own physical presence (allogenic engineers; e.g., burrows made by crayfish). Movement presents an additional challenge in quantifying legacy effects. On one hand, movements expand the spatial scope of engineering because individual organisms can create multiple modifications across the landscape (Booth et al., 2020; VanBlaricom, 1982). On the other hand, sessile foundational species, such as coral reefs, leave large, persistent legacies in single locations that are much easier to quantify. Legacies can certainly be left by organisms that are not yet dead if they engineer their environments locally but then move on. While this idea has not traditionally been included in legacy science because the effect occurs within the lifespan of the engineer, a growing body of literature highlights the need to further develop theory and experimental evidence to demonstrate how these types of effects fit into the scope of legacies. In freshwater streams, diel movements of bioturbating Sonora sucker (*Catostomus insigni*) resuspend and redistribute sediments and organic matter downriver as they feed during the night (Booth et al., 2020). In saltwater environments, stingrays excavate depressions in local tidal flats. Once abandoned, these divots provide temporary habitat for other marine fauna (Takeuchi & Tamaki, 2014). Other impressive examples include bison and wildebeest, which migrate during the growing season to browse on vegetation just as it greens up. In doing so, however, large ungulates also engineer the food resources through their browsing activity by delaying plant maturation and altering soil compaction and moisture as they graze, thereby prolonging availability of young, more nutritious vegetation on the order of weeks to months (Gass & Binkley, 2011; Geremia et al., 2019; McNaughton, 1976). Whether a legacy resulting from movement combines with or replaces a legacy resulting from death remains an exciting area for future research.

2.5 Trajectory of ecosystem engineering legacy research

A growing body of literature has described and quantified ecosystem engineering legacies, including those in the preceding sections. That legacies can arise from the activities of ecosystem engineers has been formally recognized since the seminal work by Jones et al. (1994). However, it is only recently that studies on ecosystem engineering legacies have appeared regularly in the literature. To assess the status of this research, we performed a systematic literature search in October 2021 (Appendix A; Gurevitch et al., 2001). A list of data sources used in the study are provided in the Data sources section. The number of published papers on ecosystem engineering legacies has increased steadily since the late 1990s, with a substantial increase in the past decade (Figure 2A). Although an average of 3.1 papers/year were published from 1994 to 2009, nearly 13 papers/year were published from 2010 to 2020. Interestingly, many studies did not apply the term ‘legacy’ but rather used other related terms like ‘persistence,’ ‘abandoned,’ and ‘temporal’ (Figure 2B; Appendix A). We argue that all of these terms can be usefully subsumed under the concept of ‘legacy.’ Divergent terminology likely arises, in part, from discipline-specific choices (Hodges 2008). Ecologists studying how an ecosystem engineer changes resources for communities, or landscapes, or ecosystems could all be studying legacies but might describe these alterations in different ways, such as niche construction, spatial patterns, or elemental cycling, respectively, yet all would be studying ecosystem engineering legacies. Clearly, there is large variation in ecosystem engineering legacies, and as knowledge continues to be built, we need additional synthesis and theory for identifying the ecological and environmental attributes that promote meaningful ones.

3. Toward conceptualization of legacy importance

Although recent syntheses have begun to describe ecosystem engineering effects (Albertson et al., 2015; Albertson et al., 2021; Romero et al., 2015; Woods et al., 2021), determining the importance of a legacy is complex. A legacy’s importance is influenced by non-mutually exclusive considerations of (i) the modification itself (e.g., duration), (ii) traits of the engineer (e.g., mass), and (iii) the impact on and response of the recipients that use the modified conditions (e.g., density change).In this section, we explore how to link attributes of the modification, such as duration and spatial extent, with traits of the engineer. This approach can provide new, general insights into ecosystem engineering legacies across taxa and ecosystems using a non-dimensional framework to compare different ecosystem engineers and the scale of their modifications relative to their own scaling traits.

3.1 Engineer traits determine legacy magnitude

Traits of engineering taxa will influence the characteristics of their legacy (Albertson & Allen, 2015). For example, engineers like corals that build structure or termites that have group living strategies may leave larger legacies compared to those that modify chemical properties, like salt marsh plants, or solitary organisms, like tortoises. However, it is worth noting that many traits are correlated (Boersma et al. 2016). Behavioral traits of sociality are inextricably linked to population density in termite mounds; and body size correlates to density based on resource availability and metabolic constraints (e.g., high densities of smaller bodied organisms; Elton 1927). Legacies arise from a surprisingly large number of different ecosystem engineering taxa that vary substantially in their lifespans and body sizes. Below we explore a framework that links three key traits, living strategy, lifespan, and body size, to the duration and spatial extent of the environmental modification.

3.1.1 Engineer living strategy

Categorizing engineers into those that work as individuals (e.g., a tortoise burrow), as conspecific groups (e.g., a termite mound), or as collectives illustrates what engineering characteristics lead to relatively large legacies (Figures 3). Arguably, the ecosystem engineers with the longest, and most profound legacy are the groups and collectives of cyanobacteria that produced the first free oxygen in the Earth's atmosphere during the Proterozoic era, more than

2.3 billion years ago (Lyons et al., 2014). Although cyanobacteria are still present, their current contribution to maintaining atmospheric oxygen is negligible; terrestrial plants and marine phytoplankton now produce most of the current atmospheric oxygen (Catling & Claire, 2005). This shift suggests a distinction between the legacies of engineers that cause regime shifts in biogeochemistry, and those that subsequently maintain the stability of the system. For the case of modern oxygen producing organisms, the temporal magnitude of their legacy could be represented by the 5,000 year residence time of oxygen in the atmosphere (Walker, 1980), with concentrations relatively stable over millions to 100s of millions of years (Figure 3).

3.1.2 Engineer body size

Engineer body size should be positively correlated to the spatial extent of the modification. If decay rate relates linearly to modification size, then larger modifications last longer and leave a bigger legacy because they have more material to remove. As such, larger bodied organisms likely leave bigger legacies. However, it should be noted that larger modifications may also act as bigger targets for advective forces such as wind and wave action, which could result in relatively short legacies.

3.1.3 Engineer lifespan

Engineer lifespan also contributes to legacy magnitude. Engineers that live for a long time can continually fortify the modification they make, which should result in increased duration of the modification after the engineer is gone. Longer lived organisms also have the opportunity for frequent actions through time, which may strengthen their legacy. Longer lived organisms also have larger body sizes, on average, which may lead to large legacies

(Speakman, 2005). We found that long- and short-lived organisms act as ecosystem engineers. For example, engineers that modify sediment by consolidating it or transporting it can live anywhere from fifty years (e.g, echidnas) to just one (e.g, worms; Table 2).

3.2 Synthesis of ecosystem engineering traits and legacies

We gathered data from a representative subset of the engineers identified in our literature search to compare engineering activities across different species and to quantify engineering legacies after accounting for engineer, body size, lifespan, and living strategy. We found several interesting patterns (Figure 4a; Appendix A). Several incredibly different species have similar magnitude legacies. For example, puma and earthworms have a 10-fold difference in body size and lifespan, yet they have almost identical magnitude of spatial and temporal legacy relative to their physical presence. Another example comes from conspecific groups of oysters and cordgrasses. Despite one being animal and one being plant, both species leave similar magnitude legacies.

Several species stand out as leaving especially large legacies. These include well-recognized and iconic beaver, which have high non-dimensional spatial extent, likely because of the strong response of the physical system (damming flow; trapping sediment). Coral is another example of a large legacy, with high non-dimensional temporal extent; its high non-dimensional temporal extent likely results from strong biogenic structure that can resist erosive forces.

In general, none of the engineers analyzed had both non-dimensional spatial and temporal extents less than 1.0. This finding implies that to leave a legacy, a species needs to change its environment in ways that are either as large as their body or last at least as long as their occupation time. There is also asymmetry in the pattern below 1.0 ($\log_{10} = 0$; equivalent to the body size or lifespan of the engineer) on the two axes. Many more taxa plot below 1.0 on the spatial axis than on the temporal axis. This finding shows that ecosystem engineers can have a meaningful legacy magnitude that is smaller than their body size (e.g. pit diggers such as stingray or rabbits), provided that the modification lasts longer than their time of occupation. However, the pattern does not hold in reverse. If the modification does not last long compared to occupation time, the legacy is less meaningful even it its large relative to body size. Finally, if additional studies follow the patterns we observe for these examples, we might expect a temporal threshold for individuals, as suggested by plotting position generally to the right, and a spatial threshold for groups, as suggested by plotting position generally to the top, but these distinctions are less obvious and need further investigation. Ultimately, legacies scaled to the traits of the engineer exist along a wide gradient (Figure 4b). More influential legacies are very likely left by engineers that change their environment in ways that last a long time and are large compared to their own lifespan and body size.

4. Future research directions

Because legacies have pervasive effects on biological processes, additional research will be critical for understanding how changes in abundance and richness of species that leave legacies may be altered by global change. Although legacies are increasingly studied, they still only comprise a small fraction of papers within the topic of ecosystem engineering (5% of the 3,393 results for ‘ecosystem engineer’ provided data for a legacy effect; Appendix A; Data sources section). Without considering these legacies, we may underestimate how biodiversity loss will influence ecosystem services (Chapin et al., 2000; Valiente-Banuet et al., 2015). Below we identify several exciting research directions ready for further development.

4.1 Incorporating ecological complexity

Additional considerations related to attributes of the modification, traits of the engineer, and the impact on recipient's will need to be included in future work. The mechanism of engineering, such as burrowing (loosening sediment), cementing (stabilizing sediment), or geochemical alteration, could all differentially modulate how big of a legacy is left when an engineer disappears. A previous meta-analysis shows that digging (bioturbation), for example, does not have as strong of an effect on sediments in fluvial environments as does structure building (Albertson & Allen, 2015). Bioturbation activities in particular are one obvious mechanism of ecosystem engineering that did not show up as consistently as we expected from the literature search given the well-recognized influence of bioturbating taxa such as worms or shrimps on benthic ecosystems. This finding highlights the need for additional work on how to quantify and describe bioturbation legacies, especially in marine and freshwater environments (Kristensen et al., 2012; Wilkenson et al., 2009). Future research on trait-based ecosystem engineering could assess when intraspecific engineering trait variation explains legacy size more so than interspecific traits, especially for collective legacies (Des Roches et al., 2018). The directionality of response by recipients could simultaneously be positive and negative, resulting in no net change. The response variable measured (e.g., richness, biomass, density) is an important consideration here. Recent work shows that interactions between organisms are weaker when biodiversity is measured as the response variable compared to abundance or biomass (Adams et al., 2022). As such, future research could explore how the response variable measured can control the legacy magnitude. It is worth noting that the legacies described in this paper reveal a potential observer bias. These legacies are apparent to us in part because we are large-bodied and long-lived compared to most organisms. For organisms with much smaller body sizes and shorter lifespans, more modest biotic effects in space and time qualify as important legacies. In other words, legacies can likely be scaled usefully to the size and lifespan of engineer as well as the recipients. The largest, longest-lived organisms are affected primarily by the largest-scale and most persistent modifications, whereas smaller organisms are affected by a set of smaller-scale modifications relative to their body sizes. We hope that ecosystem engineering legacy research will continue to establish how to comprehensively incorporate and weight the numerous factors that affect the magnitude and impact of an ecosystem engineering legacy.

4.2 Scale of research approaches

Most experiments or monitoring programs cannot run long enough to evaluate legacies on time scales that match the lifespan of the engineer or, even longer, the expected duration of the modification. Additionally, many studies do not cover a time period long enough to document the evolutionary consequences of an engineer altering the environment (Lenton et al. 2021; Odling-Smee et al., 2003). Rather, commonly measured responses are short-term changes in density or biomass (Albertson et al. 2021). In addition, carrying out manipulative experiments by adding or removing engineers, or experimentally altering their structures, is difficult, especially for larger-bodied engineers; the easier path is to use natural variation in presence/absence of engineers (in time or space), but those patterns can be confounded by other unrecognized or uncontrolled variables (Coggan et al., 2018). Some legacies operate on geologic time scales, where effects of now extinct taxa still persist but are not obviously associated with a specific original engineer. For example, ancient burrows likely created by ground sloths or armadillos are still visible today in South America (Frank et al., 2012; Lopes et al., 2017). Along with extinction, removal of engineers, such as reef building oysters or burrowing grouper, from the landscape can also result from anthropogenic threats such as overharvest or fishing bycatch (Coleman & Williams, 2002). Extinction of key engineers, or shifts in the relative dominance of engineering species, undoubtedly affects the role of legacies. Modeling may provide a solution to some of these challenges.

4.3 Feedbacks and modeling

Models have frequently included relationships between the environment and the engineer, but not in both directions simultaneously (Berke, 2010; Coggan et al., 2018). Such models have also traditionally focused on how individuals or species respond to a legacy rather than evaluating community or ecosystem level consequences to legacies (Berke, 2010; Cuddington et al., 2007; Zhang et al., 2012). Mechanistic models that can incorporate engineer movement and other behaviors will also be an important area of research moving forward (Franco & Fontinari, 2017; Moore, 2006). These models may be able to identify, for example, how repeated engineering activities that are more or less frequent through time can affect the magnitude of legacies. Disciplines that link ecology with the physical sciences, such as ecogeomorphology or ecohydrology, provide a novel way to place legacies into a theoretical framework that incorporates feedbacks (Atkinson et al., 2018; Corenblit et al., 2011).

Additional areas in need of development, more experimental work, and better models include projected future climate variability and facilitation (Dee et al., 2020; Silknetter et al. 2020; Vasseur et al., 2014). Global change may disrupt feedbacks between engineers and their local environments. For example, oyster larvae settle and start to grow on the shells of dead oysters, which promotes positive density dependence and the persistence of oyster beds (Moore et al., 2018). However, these relationships can be influenced by pollution, warming, and erosion of shorelines. Niche construction theory considers the ways that engineers facilitate diversity by expanding suitable conditions for other organisms (Bulleri et al., 2016; Kylafis & Loreau, 2011; Silknetter et al., 2020). Although both positive and negative outcomes for various taxa responding to altered environments created by ecosystem engineers are appreciated (Jones et al., 1997), directionality as it relates to ecological legacies remains poorly understood. For example, beaver dams might increase invertebrate beta diversity but decrease fish movement (Larsen et al. 2021). Do ‘positive’ effects have longer legacies than ‘negative’ effects, or *vice versa*, and more importantly, why? Do the processes that maintain positive legacies also maintain negative legacies? And, how will more frequent climate extremes alter the decay rates of engineered structures and their potential to support biodiversity and ecosystem processes?

4.4 Restoration and management

Restoration ecologists and land managers are capitalizing on ecosystem engineers as tools for rehabilitation (Byers et al., 2006; Crain & Bertness, 2006; Johnson et al., 2020; Law et al., 2017). Commonly used organisms include nearshore marine mollusks and large, grazing mammals that are reintroduced to areas where they were historically prominent but have been extirpated. Restored oyster beds, for example, influence availability of food resources that stimulate production of higher trophic levels and create habitat for a vast suite of other species (Borsje et al., 2011; Coen et al., 2007). Restored bison populations promote several ecosystem services and their positive effects on biodiversity are highest in abandoned rather than active wallows (Nickell et al., 2018; Wilkins et al., 2019). Effort and funding allocated to restoration work that includes ecosystem engineers suggests that practitioners are hopeful and perhaps even confident that this approach will create a persistent biogenic influence and maintain improved conditions over time. Despite these important and exciting advances, however, understanding of engineer persistence and ability to provide the anticipated restoration outcomes over the long term is still in its infancy. In an era of biodiversity loss, understanding how the removal of key ecosystem engineering organisms and their legacies will influence communities and ecosystem processes is an important area for future research in conservation biology (Boogert et al., 2006; Valiente-Banuet et al., 2015; Yeakel et al., 2020).

Literature cited

Adams, A.E., Besozzi, E.M., Shahrokhi, G., & Patten, M.A. 2022. A case for associational resistance: Apparent support for the stress gradient hypothesis varies with study system. *Ecology Letters, 25(1)*:202-217.

Albertson, L.K., & Allen, D.C. (2015). Meta-analysis: abundance, behavior, and hydraulic energy shape biotic effects on sediment transport in streams. *Ecology*, *96(5)*, 1329-1339.

Albertson, L.K., MacDonald, M.J., Tumolo, B.B., Briggs, M.A., Maguire, Z., Quinn, S., Sanchez-Ruiz, J.A., Veneros, J., & Burkle, L.A. (2021). Uncovering patterns of freshwater positive interactions using meta-analysis: Identifying the roles of common participants, invasive species and environmental context. *Ecology Letters*, *24(3)*, 594-607.

Albertson, L. K., Sklar, L. S., Tumolo, B. B., Cross, W. F., Collins, S. F., and Woods, H. A. (2022). The ghosts of ecosystem engineers: Legacy effects of biogenic modifications, Dryad, Dataset, https://doi.org/10.5061/dryad.w6m905qss.

Almond, P., Roering, J., & Hales, T.C. (2007). Using soil residence time to delineate spatial and temporal patterns of transient landscape response. *Journal of Geophysical Research: Earth Surface*, *112(F3)*.

Altermann, W. (2008). Accretion, trapping and binding of sediment in Archean stromatolites—morphological expression of the antiquity of life. *Space Science Reviews*, *135(1)*, 55-79.

Atkinson, C.L., Allen, D.C., Davis, L., & Nickerson, Z.L. (2018). Incorporating ecogeomorphic feedbacks to better understand resiliency in streams: a review and directions forward. *Geomorphology*, 305, 123-140.

Baker, M.R., Schindler, D.E., Holtgrieve, G.W., & St. Louis, V.L. (2009). Bioaccumulation and transport of contaminants: migrating sockeye salmon as vectors of mercury. *Environmental Science & Technology*, *43(23)*, 8840-8846.

Barry, J. M., Elbroch, L. M., Aiello-Lammens, M. E., Sarno, R. J., Seelye, L., Kusler, A., ... & Grigione, M. M. (2019). Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem. *Oecologia*, *189*(3), 577-586.

Basu, N.B., Van Meter, K.J., Byrnes, D.K., Van Cappellen, P., Brouwer, R., Jacobsen, B.H., Jarsjö, J., Rudolph, D.L., Cunha, M.C., Nelson, N. and Bhattacharya, R. (2022). Managing nitrogen legacies to accelerate water quality improvement. Nature Geoscience 15, 97–105.

Berke, S.K. (2010). Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integrative and Comparative Biology*, *50(2)*, 147-157.

Bergeron, Y., & Leduc, A. (1998). Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. *Journal of Vegetation Science*, *9*(4), 492-500.

Bertness, M.D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9(5)*, 191-193.

Bétard, F. (2021). Insects as zoogeomorphic agents: an extended review. *Earth Surface Processes and Landforms*, *46(1)*, 89-109.

Blankenship, R.E. (2010). Early evolution of photosynthesis. *Plant physiology*, *154(2)*, 434-438.

Boersma, K. S., Dee, L. E., Miller, S. J., Bogan, M. T., Lytle, D. A., & Gitelman, A. I. (2016). Linking multidimensional functional diversity to quantitative methods: A graphical hypothesis-evaluation framework. *Ecology*, *97*(3), 583-593.

Bologna, P. A., & Heck Jr, K. L. (1999). Macrofaunal associations with seagrass epiphytes: relative importance of trophic and structural characteristics. Journal of Experimental Marine Biology and Ecology, 242(1), 21-39.

Boogert, N.J., Paterson, D.M., & Laland, K.N. (2006). The implications of niche construction and ecosystem engineering for conservation biology. *BioScience*, *56(7)*, 570-578.

Booth, M.T., Hairston Jr, N.G., & Flecker, A.S. (2020). Consumer movement dynamics as hidden drivers of stream habitat structure: Suckers as ecosystem engineers on the night shift. *Oikos*, *129(2)*, 194-208.

Borsje, B.W., van Wesenbeeck, B.K., Dekker, F., Paalvast, P., Bouma, T.J., van Katwijk, M.M. & de Vries, M.B. (2011). How ecological engineering can serve in coastal protection. *Ecological Engineering*, *37(2)*, 113-122.

Bulleri, F., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. (2016). Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, *30(1)*, 70-78.

Bush, B. M., Stenert, C., Maltchik, L., & Batzer, D. P. (2019). Beaver-created successional gradients increase β-diversity of invertebrates by turnover in stream-wetland complexes. *Freshwater Biology*, *64*(7), 1265-1274.

Byers, J.E., Cuddington, K., Jones, C.G., Talley, T.S., Hastings, A., Lambrinos, J.G., Crooks, J.A. & Wilson, W.G. (2006). Using ecosystem engineers to restore ecological systems. *Trends in Ecology & Evolution*, *21(9)*, 493-500.

Caliman, A., Carneiro, L.S., Leal, J.J., Farjalla, V.F., Bozelli, R.L. & Esteves, F.A. (2013). Biodiversity effects of ecosystem engineers are stronger on more complex ecosystem processes. *Ecology*, 94 (9), 1977-1985.

Catalina-Allueva, P., & Martín, C. A. (2021). The role of woodpeckers (family: Picidae) as ecosystem engineers in urban parks: a case study in the city of Madrid (Spain). *Urban Ecosystems*, 1-9.

Catling, D.C., & Claire, M.W. (2005). How Earth's atmosphere evolved to an oxic state: a status report. *Earth and Planetary Science Letters*, 237(1-2), 1-20.

Cenderelli, D.A. (2000). Floods from natural and artificial dam failures E.E. Wohl (Ed.), Inland Flood Hazards: Human, Riparian and Aquatic Communities, Cambridge University Press, Cambridge, pp. 73-103

Chapin, F.S., Walker, L.R., Fastie, C.L. and Sharman, L.C. (1994). Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, *64*(2), 149-175.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E. & Mack, M.C. (2000). Consequences of changing biodiversity. *Nature*, 405(6783), 234-242.

Coen, L.D., Brumbaugh, R.D., Bushek, D., Grizzle, R., Luckenbach, M.W., Posey, M.H., Powers, S.P. & Tolley, S.G. (2007). Ecosystem services related to oyster restoration. *Marine Ecology Progress Series*, 341, 303-307.

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. *Journal of Animal Ecology*, 87(4), 974-994.

Coleman, F.C., & Williams, S.L. (2002). Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology & Evolution*, 17(1), 40-44.

Collins, S.F., Moerke, A.H., Chaloner, D.T., Janetski, D.J. & Lamberti, G.A. (2011). Response of dissolved nutrients and periphyton to spawning Pacific salmon in three northern Michigan streams. *Journal of the North American Benthological Society*, 30(3), 831-839.

Commito, J. A., Jones, B. R., Jones, M. A., Winders, S. E., & Como, S. (2019). After the fall: Legacy effects of biogenic structure on wind-generated ecosystem processes following mussel bed collapse. *Diversity*, *11*(1), 11.

Compson, Z.G., Mier, M.Z., & Marks, J.C. (2009). Effects of travertine and flow on leaf retention in Fossil Creek, Arizona. *Hydrobiologia*, 630, 187–197.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199(4335), 1302-1310.

Corenblit, D., Baas, A. C., Bornette, G., Darrozes, J., Delmotte, S., Francis, R. A., ... & Steiger, J. (2011). Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews*, *106*(3-4), 307-331.

Corenblit, D., Steiger, J., González, E., Gurnell, A. M., Charrier, G., Darrozes, J., ... & Voldoire,

O. (2014). The biogeomorphological life cycle of poplars during the fluvial biogeomorphological succession: a special focus on Populus nigra L. *Earth Surface Processes and Landforms*, *39*(4), 546-563.

Cortés-Avizanda, A., R. Jovani, J.A. Donázar, & Carrete M. (2012). Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology*, 93, 2570–2579.

Costa, A. N., Bruna, E. M., & Vasconcelos, H. L. (2018). Do an ecosystem engineer and environmental gradient act independently or in concert to shape juvenile plant communities? Tests with the leaf-cutter ant Atta laevigata in a Neotropical savanna. *PeerJ*, *6*, e5612.

Crain, C.M., & Bertness, M.D. (2006). Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience*, 56(3), 211-218.

Cribb, A.T. and Bottjer, D.J. (2020). Complex marine bioturbation ecosystem engineering behaviors persisted in the wake of the end-Permian mass extinction. *Scientific reports*, *10*(1), 1-8.

Cuddington, K. (2011). Legacy effects: the persistent impact of ecological interactions. *Biological Theory*, 6(3), 203-210.

Cuddington, K., Byers, J.E., Wilson, W.G., & Hastings A. eds. (2007). Ecosystem Engineers: Plants to Protists. Academic Press. 442 pages.

Daleo, P., Escapa, M., Alberti, J., & Iribarne, O. (2006). Negative effects of an autogenic ecosystem engineer: interactions between coralline turf and an ephemeral green alga. *Marine Ecology Progress Series*, 315, 67-73.

Dawkins, R. (1982). *The extended phenotype* (Vol. 8). Oxford: Oxford university press.

Dawson, S. J., Broussard, L., Adams, P. J., Moseby, K. E., Waddington, K. I., Kobryn, H. T., ... & Fleming, P. A. (2019). An outback oasis: the ecological importance of bilby burrows. *Journal of Zoology*, *308*(3), 149-163.

D'Andrea, A. F., Aller, R. C., & Lopez, G. R. (2002). Organic matter flux and reactivity on a South Carolina sandflat: The impacts of porewater advection and macrobiological structures. *Limnology and Oceanography*, *47*(4), 1056-1070.

Decaëns, T., & Rossi, J. P. (2001). Spatio–temporal structure of earthworm community and soil heterogeneity in a tropical pasture. *Ecography*, *24*(6), 671-682.

Dee, L.E., Okamtoto, D., Gårdmark, A., Montoya, J.M. & Miller, S.J. (2020). Temperature variability alters the stability and thresholds for collapse of interacting species. *Philosophical Transactions of the Royal Society B*, 375(1814), 20190457.

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., ... & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, *2*(1), 57-64.

Dietrich, W.E., & Perron, J.T. (2006). The search for a topographic signature of life. *Nature*, 439(7075), 411-418.

Doody, J.S., Soennichsen, K.F., James, H., McHenry, C. & Clulow, S. (2021). Ecosystem engineering by deep-nesting monitor lizards. *Ecology*, pp.e03271-e03271.

Drury, W.H. and Nisbet, I.C. (1973). Succession. Journal of the Arnold arboretum, 54(3), 331-368.

Dunson, W.A., & Travis, J. (1991). The role of abiotic factors in community organization. *The American Naturalist*, 138(5), 1067-1091.

Ebert, D., Hottinger, J. W., & Pajunen, V. I. (2013). Unsuitable habitat patches lead to severe underestimation of dynamics and gene flow in a zooplankton metapopulation. *Journal of animal ecology*, *82*(4), 759-769.

Edwards, S.C., Shoot, T.T., Martin, R.J., Sherry, D.F., & Healy, S.D. (2020). It's not all about temperature: breeding success also affects nest design. *Behavioral Ecology* 31(4), 1065-1072.

Eisenhauer, N. (2010). The action of an animal ecosystem engineer: identification of the main mechanisms of earthworm impacts on soil microarthropods. *Pedobiologia*, 53(6), 343-352.

Eldridge, D. J., & Koen, T. B. (2021). Temporal changes in soil function in a wooded dryland following simulated disturbance by a vertebrate engineer. *Catena*, *200*, 105166.

Elton, C. S. (1927). *Animal ecology*. University of Chicago Press.

Estes, J.A., & Vermeij, G.J. (2022). History's legacy: Why future progress in ecology demands a view of the past. Ecology. In press.

Farji-Brener, A.G., & Werenkraut, V. (2015). A meta-analysis of leaf-cutting ant nest effects on soil fertility and plant performance. *Ecological Entomology*, 40(2), 150-158.

Ferris, F.G., Fratton, C.M., Gerits, J.P., Schultze-Lam, S., & Lollar, B.S. (1995). Microbial precipitation of a strontium calcite phase at a groundwater discharge zone near Rock Creek, British Columbia, Canada.*Geomicrobiology Journal*, 13, 57-67.

Franco, C., & Fontanari, J.F. (2017). The spatial dynamics of ecosystem engineers. *Mathematical biosciences*, 292, 76-85.

Frank, H.T., Buchmann, F.S.C., Lima, L.G., Fornari, M., Caron, F. & Lopes, R.P. (2012). Cenozoic vertebrate tunnels in Southern Brazil. *Ichnology of Latin America: selected papers*, 2, 141-158.

Frauendorf, T.C, Subalusky, A.L., Dutton, C.L., Hamilton, S.K., Masese, F.O., Rosi, E.J., Singer, G.A., & Post, D.M. (2021). Animal legacies lost and found in river ecosystems. *Environmental Research Letters*, *16*, 115011.

Frelich, L. E., Blossey, B., Cameron, E. K., Dávalos, A., Eisenhauer, N., Fahey, T., ... & Reich, P. B. (2019). Side-swiped: ecological cascades emanating from earthworm invasions. *Frontiers in Ecology and the Environment*, *17*(9), 502-510.

Fremier, A.K., Yanites, B.J. & Yager, E.M. (2018). Sex that moves mountains: The influence of spawning fish on river profiles over geologic timescales. *Geomorphology*, *305*, 163-172.

Friend, P. L., Collins, M. B., & Holligan, P. M. (2003). Day–night variation of intertidal flat sediment properties in relation to sediment stability. *Estuarine, Coastal and Shelf Science*, 58(3), 663-675.

Fournier, V., Rosenheim, J. A., Brodeur, J., Laney, L. O., & Johnson, M. W. (2003). Herbivorous mites as ecological engineers: indirect effects on arthropods inhabiting papaya foliage. *Oecologia*, *135*(3), 442-450.

Fuller, B.M., Sklar, L.S., Compson, Z.G., Adams, K.J., Marks, J.C., & Wilcox, A. C. (2011). Ecogeomorphic feedbacks in regrowth of travertine step-pool morphology after dam decommissioning, Fossil Creek, Arizona. *Geomorphology*, *126(3-4)*, 314-332.

Gass, T.M. and Binkley, D. (2011). Soil nutrient losses in an altered ecosystem are associated with native ungulate grazing. *Journal of Applied Ecology*, *48*(4), 952-960.

Geremia, C., Merkle, J.A., Eacker, D.R., Wallen, R.L., White, P.J., Hebblewhite, M. & Kauffman, M.J. (2019). Migrating bison engineer the green wave. *Proceedings of the National Academy of Sciences*, *116(51)*, 25707-25713.

Gerig, B.S., Chaloner, D.T., Janetski, D.J., Rediske, R.R., O'Keefe, J.P., Moerke, A.H. & Lamberti, G.A. (2016). Congener patterns of persistent organic pollutants establish the extent of contaminant biotransport by Pacific salmon in the Great Lakes. *Environmental Science & Technology*, *50(2)*, 554-563.

Germain, R.M., Mayfield, M.M. & Gilbert, B. (2018). The 'filtering'metaphor revisited: competition and environment jointly structure invasibility and coexistence. Biology letters, 14(8), 20180460.

Gribben, P.E., Byers, J.E., Wright, J.T. & Glasby, T.M. (2013). Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem. *Oikos*, *122(6)*, 816-824.

Gurevitch, J., Curtis, P.S., & Jones, M.H. (2001). "Meta-analysis in ecology," in *Advances in Ecological Research 32*, 199-247.

Guo, Q. (1996). Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia*, *106*(2), 247-256.

Gutiérrez, J. L., & Jones, C. G. (2006). Physical ecosystem engineers as agents of biogeochemical heterogeneity. *BioScience*, *56*(3), 227-236.

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(2)*, 153-164.

Haupt, T. M., Sinclair, B. J., Shaw, J. D., & Chown, S. L. (2016). Further support for thermal ecosystem engineering by wandering albatross. *Antarctic Science*, *28*(1), 35-43.

Hierro, J. L., Clark, K. L., Branch, L. C., & Villarreal, D. (2011). Native herbivore exerts contrasting effects on fire regime and vegetation structure. *Oecologia*, *166*(4), 1121-1129.

Hodges, K.E. (2008). Defining the problem: terminology and progress in ecology. *Frontiers in Ecology and the Environment*, *6(1)*, 35-42.

Hogg, R. S., Coghlan Jr, S. M., Zydlewski, J., & Simon, K. S. (2014). Anadromous sea lampreys (*Petromyzon marinus*) are ecosystem engineers in a spawning tributary. *Freshwater Biology*, *59*(6), 1294-1307.

Holdsworth, A.R., Frelich, L.E., & Reich, P.B. (2007). Effects of earthworm invasion on plant species richness in northern hardwood forests. *Conservation Biology*, *21(4)*, 997-1008.

Hughes, T.P., Kerry, J.T., Connolly, S.R., Baird, A.H., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Jacobson, M., Liu, G. and Pratchett, M.S., 2019. Ecological memory modifies the cumulative impact of recurrent climate extremes. Nature Climate Change, 9(1), pp.40-43.

Huntzinger, M., Karban, R., & Maron, J. L. (2011). Small mammals cause non-trophic effects on habitat and associated snails in a native system. *Oecologia*, *167*(4), 1085-1091.

Ilarri, M. I., Souza, A. T., Amorim, L., & Sousa, R. (2019). Decay and persistence of empty bivalve shells in a temperate riverine system. *Science of the Total Environment*, *683*, 185-192.

Jackson- Bué, T., Williams, G. J., Walker-Springett, G., Rowlands, S. J., & Davies, A. J. (2021).

Three- dimensional mapping reveals scale- dependent dynamics in biogenic reef habitat structure. *Remote Sensing in Ecology and Conservation 7(4):*621-637.

James, A. I., Eldridge, D. J., Koen, T. B., & Moseby, K. E. (2011). Can the invasive European rabbit (*Oryctolagus cuniculus*) assume the soil engineering role of locally-extinct natives?. *Biological Invasions*, *13*(12), 3027-3038.

Johnson, M.F., Thorne, C.R., Castro, J.M., Kondolf, G.M., Mazzacano, C.S., Rood, S.B. & Westbrook, C. (2020). Biomic river restoration: A new focus for river management. *River Research and Applications 36*, 3-12.

Johnson-Bice, S.M., Gable, T.D., Windels, S.K., & Horst, G.E. (2022). Relics of beavers past: time and population density drive scale-dependent patterns of ecosystem engineering. *Ecography*. In press.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L. and Schoennagel, T. (2016). Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment, 14(7), 369-378.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. In *Ecosystem Management* (pp. 130-147). Springer, New York, NY.

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, *78*(7), 1946-1957.

Joseph, G. S., Seymour, C. L., Coetzee, B. W., Ndlovu, M., Deng, L., Fowler, K., ... & Foord, S. H. (2018). Elephants, termites and mound thermoregulation in a progressively warmer world. *Landscape ecology*, *33*(5), 731-742.

Kannenberg, S.A., Schwalm, C.R. and Anderegg, W.R. (2020). Ghosts of the past: how drought legacy effects shape forest functioning and carbon cycling. Ecology Letters, 23(5), 891-901.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O. and Banta, G.T. (2012). What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Marine Ecology Progress Series, 446, 285-302.

Kylafis, G., & Loreau, M. (2011). Niche construction in the light of niche theory. *Ecology Letters*, *14(2)*, 82-90.

Laidre, M.E., & Greggor, A.L. (2015). Swarms of swift scavengers: ecological role of marine intertidal hermit crabs in California. *Marine Biology*, *162(5)*, 969-977.

Lane, S.J., Moran, A.L., Shishido, C.M., Tobalske, B.W., & Woods, H.A. (2018). Cuticular gas exchange by Antarctic sea spiders. *Journal of Experimental Biology*, *221(8)*, jeb177568.

Lane, S.J., Shishido, C.M., Moran, A.L., Tobalske, B.W., & Woods, H.A. (2016). No effects and no control of epibionts in two species of temperate pycnogonids. *The Biological Bulletin*, *230(2)*, 165-173.

Larsen, A., Larsen, J. R., & Lane, S. N. (2021). Dam builders and their works: Beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems. Earth-Science Reviews, 218, 103623.

Laurel, D., & Wohl, E. (2019). The persistence of beaver-induced geomorphic heterogeneity and organic carbon stock in river corridors. *Earth Surface Processes and Landforms*, *44*(1), 342-353.

Lavelle, P. (2002). Functional domains in soils. *Ecological Research, 17(4)*, 441-450.

Lavelle, P., Barot, S., Blouin, M., Decaëns, T., Jimenez, J. J., & Jouquet, P. (2007). Earthworms as key actors in self-organized soil systems. *Ecosystem Engineers: Plants to Protists*, *4,* 77-106.

Law, A., Gaywood, M.J., Jones, K.C., Ramsay, P. & Willby, N.J. (2017). Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. *Science of the Total Environment*, *605*, 1021-1030.

Lenton, T.M., Kohler, T.A., Marquet, P.A., Boyle, R.A., Crucifix, M., Wilkinson, D.M. & Scheffer, M. (2021). Survival of the Systems. *Trends in Ecology & Evolution, 36(4)*, 333-344.

Liermann, L.J., Albert, I., Buss, H.L., Minyard, M., & Brantley, S. L. (2015). Relating microbial community structure and geochemistry in deep regolith developed on volcaniclastic rock in the Luquillo Mountains, Puerto Rico. *Geomicrobiology Journal*, *32(6)*, 494-510.

Lill, J. T., & Marquis, R. J. (2003). Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology*, *84*(3), 682-690.

Lima, A.T., Mitchell, K., O'Connell, D.W., Verhoeven, J. and Van Cappellen, P. (2016). The legacy of surface mining: Remediation, restoration, reclamation and rehabilitation. Environmental Science & Policy, 66, 227-233.

Lopes, R.P., Frank, H.T., Buchmann, F.S.D.C., & Caron, F. (2017). *Megaichnus igen*. nov.: giant paleoburrows attributed to extinct Cenozoic mammals from South America. *Ichnos*, *24(2)*, 133-145.

Lopez, J.W., Parr, T.B., Allen, D.C., & Vaughn, C.C. (2020). Animal aggregations promote emergent aquatic plant production at the aquatic–terrestrial interface. *Ecology*, *101(10),* e03126.

Loranger, G., Ponge, J.F., Blanchart, E., & Lavelle, P. (1998). Impact of earthworms on the diversity of microarthropods in a vertisol (Martinique). *Biology and Fertility of Soils, 27(1)*, 21-26.

Lyons, T. W., Reinhard, C. T., & Planavsky, N. J. (2014). The rise of oxygen in Earth's early ocean and atmosphere. *Nature*, *506(7488)*, 307-315.

Marshall, F., Reid, R.E., Goldstein, S., Storozum, M., Wreschnig, A., Hu, L., Kiura, P., Shahack-Gross, R. & Ambrose, S.H. (2018). Ancient herders enriched and restructured African grasslands. *Nature*, *561(7723)*, 387-390.

McNaughton, S. J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science, *191(4222)*, 92-94.

Meigs, G. W., Zald, H. S., Campbell, J. L., Keeton, W. S., & Kennedy, R. E. (2016). Do insect outbreaks reduce the severity of subsequent forest fires?. *Environmental Research Letters*, *11*(4), 045008.

Merz-Preis, M., & Riding, R. (1999). Cyanobacterial tufa calcification in two freshwater streams: ambient environment, chemical thresholds and biological processes. *Sedimentary Geology*, *126(1-4)*, 103–124.

Messmer, V., Jones, G.P., Munday, P.L., Holbrook, S.J., Schmitt, R.J., & Brooks, A.J. (2011). Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology, 92(12)*, 2285-2298.

Miller, T.E., TerHorst, C.P. & Burns, J.H. (2009). The ghost of competition present. *The American Naturalist, 173(3)*, 347-353.

Moore, J. W. (2006). Animal ecosystem engineers in streams. *BioScience*, *56*(3), 237-246.

Moore, J.L., Puckett, B.J. & Schreiber, S.J. (2018). Restoration of eastern oyster populations with positive density dependence. *Ecological Applications*, *28(4)*, 897-909.

Morrissey, C.A., Pollet, I.L., Ormerod, S.J. & Elliott, J.E. (2012). American dippers indicate contaminant biotransport by Pacific salmon. *Environmental Science & Technology*, *46(2)*, 1153-1162.

Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American streams by beaver. *BioScience*, *38*(11), 753-762.

Naiman, R. J., Melillo, J. M., & Hobbie, J. E. (1986). Ecosystem alteation of boreal forest streams by beaver (Castor canadensis). *Ecology*, *67*(5), 1254-1269.

Napieralski, S.A., Buss, H.L., Brantley, S.L., Lee, S., Xu, H., & Roden, E.E. (2019). Microbial chemolithotrophy mediates oxidative weathering of granitic bedrock. *Proceedings of the National Academy of Sciences*, *116(52)*, 26394-26401.

Naylor, L.A., Viles, H.A. & Carter, N.E.A. (2002). Biogeomorphology revisited: looking towards the future. *Geomorphology*, *47(1)*, 3-14.

Nickell, Z., Varriano, S., Plemmons, E., & Moran, M.D. (2018). Ecosystem engineering by bison (*Bison bison*) wallowing increases arthropod community heterogeneity in space and time. *Ecosphere*, *9(9)*, e02436.

Novoa, A., González, L., Moravcová, L., & Pyšek, P. (2013). Constraints to native plant species establishment in coastal dune communities invaded by Carpobrotus edulis: Implications for restoration. *Biological Conservation*, *164*, 1-9.

Odling-Smee, F. John, Kevin N. Laland, and Marcus W. Feldman. (1996). Niche construction. *The American Naturalist, 147(4)*, 641-648.

Odling-Smee, F.J., Laland K.N., & Feldman, M.W. (2003). Niche Construction: A Neglected Process in Evolution. Princeton (NJ): Princeton University Press.

Odum, E.P. (1969). The Strategy of Ecosystem Development: An understanding of ecological succession provides a basis for resolving man's conflict with nature. Science, 164(3877), 262-270.

Paterson, D.M., Aspden, R.J., Visscher, P.T., Consalvey, M., Andres, M.S., Decho, A.W., Stolz, J. & Reid, R.P. (2008). Light-dependant biostabilisation of sediments by stromatolite assemblages. *PLoS One*, *3(9)*, e3176.

Pentecost, A., 2005. *Travertine*. Springer Science & Business Media.

Pincebourde, S., & Casas, J. (2019). Narrow safety margin in the phyllosphere during thermal extremes. *Proceedings of the National Academy of Sciences, 116(12)*, 5588-5596.

Pringle, R.M. (2008). Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology*, *89*(1), 26-33.

Prugh, L. R., & Brashares, J. S. (2012). Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. *Journal of Animal Ecology*, 667-678.

Reise, K., Buschbaum, C., Büttger, H., Rick, J., & Wegner, K. M. (2017). Invasion trajectory of Pacific oysters in the northern Wadden Sea. *Marine biology*, *164*(4), 68.

Rex, J.F., Petticrew, E.L., Albers, S.J. and Williams, N.D. (2014). The influence of Pacific salmon decay products on near-field streambed sediment and organic matter dynamics: a flume simulation. Earth Surface Processes and Landforms, 39(10), 1378-1385.

Rice, S.P. (2021). Why so skeptical? The role of animals in fluvial geomorphology. *Wiley Interdisciplinary Reviews: Water*, *8*, e1549.

Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J.B., Nicol, S., Pershing, A. and Smetacek, V. (2014). Whales as marine ecosystem engineers. *Frontiers in Ecology and the Environment*, *12*(7), pp.377-385.

Romero, G.Q., Gonçalves-Souza, T., Vieira, C. & Koricheva, J. (2015). Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*, *90(3)*, 877-890.

Ross, C. E., McIntyre, S., Barton, P. S., Evans, M. J., Cunningham, S. A., & Manning, A. D. (2020). A reintroduced ecosystem engineer provides a germination niche for native plant species. *Biodiversity and Conservation*, *29*(3), 817-837.

Rutherford W.H. (1953). Effects of a summer flash flood upon a beaver population. *Journal of Mammalogy*, *34(2)*, 261-262.

Scatena, F.N., & Lugo, A.E. (1995). Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. *Geomorphology*, *13(1-4)*, 199-213.

Schoenian, I., Spiteller, M., Ghaste, M., Wirth, R., Herz, H., & Spiteller, D. (2011). Chemical basis of the synergism and antagonism in microbial communities in the nests of leaf-cutting ants. *Proceedings of the National Academy of Sciences*, *108(5)*, 1955-1960.

Silknetter, S., Creed, R.P., Brown, B.L., Frimpong, E.A., Skelton, J. & Peoples, B.K. (2020). Positive biotic interactions in freshwaters: A review and research directive. *Freshwater Biology*, *65(4)*, 811-832.

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*(1), 251-262.

Smith, C.R., Glover, A.G., Treude, T., Higgs, N.D., & Amon, D.J. (2015). Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. *Annual Review of Marine Science*, *7*, 571-596.

Speakman, J.R. (2005). Body size, energy metabolism and lifespan. Journal of Experimental Biology, 208(9), 1717-1730.

Stavi, I., Zaady, E., Gusarov, A., & Yizhaq, H. (2021). Dead shrub patches as ecosystem engineers in degraded drylands. *Journal of Geographical Sciences*, *31*(8), 1187-1204.

Takashima, C. & Kano, A. (2008). Microbial processes forming daily lamination in a stromatolitic travertine. *Sedimentary Geology*, *208(3-4)*, 114–119.

Takeuchi, S., & Tamaki, A. (2014). Assessment of benthic disturbance associated with stingray foraging for ghost shrimp by aerial survey over an intertidal sandflat. *Continental Shelf Research*, *84*, 139-157.

Theenhaus, A. & Scheu, S. (1996). The influence of slug (*Arion rufus*) mucus and cast material addition on microbial biomass, respiration, and nutrient cycling in beech leaf litter. *Biology and Fertility of Soils*, *23(1)*, 80-85.

Thomsen, M.S., Altieri, A.H., Angelini, C., Bishop, M.J., Gribben, P.E., Lear, G., He, Q., Schiel, D.R., Silliman, B.R., South, P.M. & Watson, D.M. (2018). Secondary foundation species enhance biodiversity. *Nature Ecology & Evolution*, *2(4)*, 634-639.

Thomsen, M.S., Wernberg, T., Altieri, A., 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(2)*, 158-175.

Thorp, J. H. (1988). Patches and the responses of lake benthos to sunfish nest-building. *Oecologia*, *76*(2), 168-174.

Tumolo, B. B., Albertson, L. K., Cross, W. F., Daniels, M. D., & Sklar, L. S. (2019). Occupied and abandoned structures from ecosystem engineering differentially facilitate stream community colonization. *Ecosphere*, *10*(5), e02734.

Valentine, L. E., Ruthrof, K. X., Fisher, R., Hardy, G. E. S. J., Hobbs, R. J., & Fleming, P. A. (2018). Bioturbation by bandicoots facilitates seedling growth by altering soil properties. *Functional Ecology*, *32*(9), 2138-2148.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P. & Medel, R. (2015). Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, *29(3)*, 299-307.

VanBlaricom, G. R. (1982). Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecological Monographs*, *52*(3), 283-305.

Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D., McCann, K.S., Savage, V., Tunney, T.D. & O'Connor, M.I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences*, *281(1779)*, 20132612.

Verspoor, J.J., Braun, D.C. and Reynolds, J.D. (2010). Quantitative links between Pacific salmon and stream periphyton. *Ecosystems*, *13*(7), 1020-1034.

Verspoor, J.J., Braun, D.C., Stubbs, M.M. & Reynolds, J.D. (2011). Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities. *Ecosphere*, *2(2)*, 1-17.

Viles, H., & Pentecost, A. (1999). Geomorphological controls on tufa deposition at Nash

Brook, South Wales, United Kingdom. *Cave and Karst Science*, *26(2)*, 61–68.

Von Holle, B., Neill, C., Largay, E. F., Budreski, K. A., Ozimec, B., Clark, S. A., & Lee, K. (2013). Ecosystem legacy of the introduced N 2-fixing tree *Robinia pseudoacacia* in a coastal forest. *Oecologia*, *172*(3), 915-924.

Walker, J.C. (1980). "The Oxygen Cycle". The Natural Environment and the Biogeochemical Cycles. The Handbook of Environmental Chemistry. Springer Berlin Heidelberg. pp. 87–104.

Wilby, A., Shachak, M. and Boeken, B., 2001. Integration of ecosystem engineering and trophic effects of herbivores. Oikos, 92(3), pp.436-444.

Wilkins, K., Pejchar, L. & Garvoille, R. (2019). Ecological and social consequences of bison reintroduction in Colorado. *Conservation Science and Practice*, *1(2)*, p.e9.

Wilkinson, M.T., Richards, P.J. and Humphreys, G.S. (2009). Breaking ground: pedological, geological, and ecological implications of soil bioturbation. Earth-Science Reviews, 97(1-4), 257-272.

Willenbring, J. K., Codilean, A. T., & McElroy, B. (2013). Earth is (mostly) flat: Apportionment of the flux of continental sediment over millennial time scales. *Geology*, *41(3)*, 343-346.

Wittenberg, J. (2013). What is a historical legacy? In *APSA 2013 Annual Meeting Paper, American Political Science Association 2013 Annual Meeting*.

Wohl, E. (2019). Forgotten legacies: understanding and mitigating historical human alterations of river corridors. *Water Resources Research*, *55(7)*, 5181-5201.

Wohl, E. (2021). Legacy effects of loss of beavers in the continental United States. *Environmental Research Letters*, *16*(2), 025010.

Włodarska-Kowalczuk, M., Jankowska, E., Kotwicki, L., & Balazy, P. (2014). Evidence of season-dependency in vegetation effects on macrofauna in temperate seagrass meadows (Baltic Sea). *PLoS One*, *9*(7), e100788.

Woo, M.K., & Waddington, J.M. (1990). Effects of beaver dams on subarctic wetland hydrology. *Arctic*, *43(3)*, 223–230.

Woods, H.A., Pincebourde, S., Dillon, M.E. and Terblanche, J.S. (2021). Extended phenotypes: buffers or amplifiers of climate change? *Trends in Ecology & Evolution,* 36, 889-898.

Wright, J.P. and Jones, C.G. (2006). The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *BioScience*, *56*(3), pp.203-209.

Yeakel, J. D., Pires, M. M., de Aguiar, M. A., O'Donnell, J. L., Guimarães, P. R., Gravel, D., & Gross, T. (2020). Diverse interactions and ecosystem engineering can stabilize community assembly. Nature communications, *11(1)*, 1-10.

Zangerlé, A., Hissler, C., Blouin, M., & Lavelle, P. (2014). Near infrared spectroscopy (NIRS) to estimate earthworm cast age. *Soil Biology and Biochemistry*, *70*, 47-53.

Data sources

Papers included in Figure 2, arranged in this list by chronological order.

1. Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences*, *96*(18), 10242-10247.
2. Decaëns, T., & Rossi, J. P. (2001). Spatio–temporal structure of earthworm community and soil heterogeneity in a tropical pasture. *Ecography*, *24*(6), 671-682.
3. Reichman, O. J., & Seabloom, E. W. (2002). The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology & Evolution*, *17*(1), 44-49.
4. Gilkinson, K. D., Fader, G. B. J., Gordon Jr, D. C., Charron, R., McKeown, D., Roddick, D., ... & Liu, Q. (2003). Immediate and longer-term impacts of hydraulic clam dredging on an offshore sandy seabed: effects on physical habitat and processes of recovery. *Continental Shelf Research*, *23*(14-15), 1315-1336.
5. Wright, J. P., Flecker, A. S., & Jones, C. G. (2003). Local vs. landscape controls on plant species richness in beaver meadows. *Ecology*, *84*(12), 3162-3173.
6. Berkenbusch, K., & Rowden, A. A. (2003). Ecosystem engineering—moving away from'just-so'stories. *New Zealand Journal of Ecology*, 67-73.
7. Day, R. L., Laland, K. N., & Odling-Smee, F. J. (2003). Rethinking adaptation: the niche-construction perspective. *Perspectives in biology and medicine*, *46*(1), 80-95.

8. Laland, K. N. (2004). Extending the extended phenotype. *Biology and Philosophy*, *19*(3), 313-325.
9. Hui, C., Li, Z., & Yue, D. X. (2004). Metapopulation dynamics and distribution, and environmental heterogeneity induced by niche construction. *Ecological Modelling*, *177*(1-2), 107-118.
10. Wright, J. P., Gurney, W. S., & Jones, C. G. (2004). Patch dynamics in a landscape modified by ecosystem engineers. *Oikos*, *105*(2), 336-348.
11. Laland, K. N., Odling-Smee, J., & Feldman, M. W. (2005). On the breadth and significance of niche construction: a reply to Griffiths, Okasha and Sterelny. *Biology and Philosophy*, *20*(1), 37-55.
12. Valdivia-Hoeflich, T., Vega Rivera, J. H., & Stoner, K. E. (2005). The Citreoline Trogon as an Ecosystem Engineer 1. *Biotropica: The Journal of Biology and Conservation*, *37*(3), 465-467.
13. Dostál, P., Březnová, M., Kozlíčková, V., Herben, T., & Kovář, P. (2005). Ant-induced soil modification and its effect on plant below-ground biomass. *Pedobiologia*, *49*(2), 127-137.
14. Gorosito, N. B., Curmi, P., Hallaire, V., Folgarait, P. J., & Lavelle, P. M. (2006). Morphological changes in Camponotus punctulatus (Mayr) anthills of different ages. *Geoderma*, *132*(3-4), 249-260.
15. Stallins, J. A. (2006). Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. *Geomorphology*, *77*(3-4), 207-216.
16. Kawai, T., & Tokeshi, M. (2006). Asymmetric coexistence: bidirectional abiotic and biotic effects between goose barnacles and mussels. *Journal of Animal Ecology*, *75*(4), 928-941.
17. Corenblit, D., Tabacchi, E., Steiger, J., & Gurnell, A. M. (2007). Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. *Earth-Science Reviews*, *84*(1-2), 56-86.
18. Wolf, E. C., Cooper, D. J., & Hobbs, N. T. (2007). Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications*, *17*(6), 1572-1587.
19. Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., ... & Wilson, W. G. (2007). Ecosystem engineering in space and time. *Ecology letters*, *10*(2), 153-164.
20. Corenblit, D., Gurnell, A. M., Steiger, J., & Tabacchi, E. (2008). Reciprocal adjustments between landforms and living organisms: extended geomorphic evolutionary insights. *Catena*, *73*(3), 261-273.
21. DeFauw, S. L., Vogt, J. T., & Boykin, D. L. (2008). Influence of mound construction by red and hybrid imported fire ants on soil chemical properties and turfgrass in a sod production agroecosystem. *Insectes sociaux*, *55*(3), 301-312.
22. Paterson, D. M., Aspden, R. J., Visscher, P. T., Consalvey, M., Andres, M. S., Decho, A. W., ... & Reid, R. P. (2008). Light-dependant biostabilisation of sediments by stromatolite assemblages. *PLoS One*, *3*(9), e3176.
23. de Vries, M. B., & Borsje, B. W. (2008). Species response to climate change could affect the fate of fine sediment in the Wadden Sea.
24. Erwin, D. H. (2008). Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in ecology & evolution*, *23*(6), 304-310.

25. Krakauer, D. C., Page, K. M., & Erwin, D. H. (2009). Diversity, dilemmas, and monopolies of niche construction. *The American Naturalist*, *173*(1), 26-40.
26. Beckage, B., Platt, W. J., & Gross, L. J. (2009). Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. *The American Naturalist*, *174*(6), 805-818.
27. Conser, C., & Connor, E. F. (2009). Assessing the residual effects of Carpobrotus edulis invasion, implications for restoration. *Biological invasions*, *11*(2), 349-358.
28. Wright, J. P. (2009). Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer. *Ecology*, *90*(12), 3418-3429.
29. Schmidt, I., Leuschner, C., Mölder, A., & Schmidt, W. (2009). Structure and composition of the seed bank in monospecific and tree species-rich temperate broad-leaved forests. *Forest Ecology and Management*, *257*(2), 695-702.
30. Phillips, J. D. (2009). Soils as extended composite phenotypes. *Geoderma*, *149*(1-2), 143-151.
31. Corenblit, D., Steiger, J., Gurnell, A. M., & Naiman, R. J. (2009). Plants intertwine fluvial landform dynamics with ecological succession and natural selection: a niche construction perspective for riparian systems. *Global Ecology and Biogeography*, *18*(4), 507-520.
32. 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*(1), 27-35.
33. Eldridge, D. J., Whitford, W. G., & Duval, B. D. (2009). Animal disturbances promote shrub maintenance in a desertified grassland. *Journal of Ecology*, *97*(6), 1302-1310.
34. Schulte, D. M., Burke, R. P., & Lipcius, R. N. (2009). Unprecedented restoration of a native oyster metapopulation. *Science*, *325*(5944), 1124-1128.
35. Kinhal, V., & Parthasarathy, N. (2010). Nucleated succession by an endemic palm Phoenix pusilla enhances diversity of woody species in the arid Coromandel Coast of India. *AoB Plants*, *2010*.
36. Laland, K. N., & Boogert, N. J. (2010). Niche construction, co-evolution and biodiversity. *Ecological economics*, *69*(4), 731-736.
37. Verspoor, J. J., Braun, D. C., & Reynolds, J. D. (2010). Quantitative links between Pacific salmon and stream periphyton. *Ecosystems*, *13*(7), 1020-1034.
38. Padisák, J., Hajnal, E., Krienitz, L., Lakner, J., & Üveges, V. (2010). Rarity, ecological memory, rate of floral change in phytoplankton—and the mystery of the Red Cock. In *Fifty years after the ''Homage to Santa Rosalia'': Old and new paradigms on biodiversity in aquatic ecosystems* (pp. 45-64). Springer, Dordrecht.
39. McKey, D., Rostain, S., Iriarte, J., Glaser, B., Birk, J. J., Holst, I., & Renard, D. (2010). Pre-Columbian agricultural landscapes, ecosystem engineers, and self-organized patchiness in Amazonia. *Proceedings of the National Academy of Sciences*, *107*(17), 7823-7828.
40. Griffiths, C. J., Jones, C. G., Hansen, D. M., Puttoo, M., Tatayah, R. V., Müller, C. B., & Harris, S. (2010). The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. *Restoration Ecology*, *18*(1), 1-7.
41. Mathieu, J., Barot, S., Blouin, M., Caro, G., Decaëns, T., Dubs, F., ... & Nai, P. (2010). Habitat quality, conspecific density, and habitat pre-use affect the dispersal behaviour of two earthworm species, Aporrectodea icterica and Dendrobaena veneta, in a mesocosm experiment. *Soil Biology and Biochemistry*, *42*(2), 203-209.

42. James, A. I., Eldridge, D. J., Koen, T. B., & Moseby, K. E. (2011). Can the invasive European rabbit (Oryctolagus cuniculus) assume the soil engineering role of locally-extinct natives?. *Biological Invasions*, *13*(12), 3027-3038.
43. Irigoyen, A. J., Trobbiani, G., Sgarlatta, M. P., & Raffo, M. P. (2011). Effects of the alien algae Undaria pinnatifida (Phaeophyceae, Laminariales) on the diversity and abundance of benthic macrofauna in Golfo Nuevo (Patagonia, Argentina): potential implications for local food webs. *Biological Invasions*, *13*(7), 1521-1532.
44. Cuddington, K. (2011). Legacy effects: the persistent impact of ecological interactions. *Biological Theory*, *6*(3), 203-210.
45. Corenblit, D., Baas, A. C., Bornette, G., Darrozes, J., Delmotte, S., Francis, R. A., ... & Steiger, J. (2011). Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews*, *106*(3-4), 307-331.
46. Błędzki, L. A., Bubier, J. L., Moulton, L. A., & Kyker-Snowman, T. D. (2011). Downstream effects of beaver ponds on the water quality of New England first-and second-order streams. *Ecohydrology*, *4*(5), 698-707.
47. Dunham, A. E. (2011). Soil disturbance by vertebrates alters seed predation, movement and germination in an African rain forest. *Journal of Tropical ecology*, *27*(6), 581-589.
48. Crowe, T. P., Frost, N. J., & Hawkins, S. J. (2011). Interactive effects of losing key grazers and ecosystem engineers vary with environmental context. *Marine ecology progress series*, *430*, 223-234.
49. Wall, C. C., Donahue, B. T., Naar, D. F., & Mann, D. A. (2011). Spatial and temporal variability of red grouper holes within Steamboat Lumps Marine Reserve, Gulf of Mexico. *Marine Ecology Progress Series*, *431*, 243-254.
50. Hierro, J. L., Clark, K. L., Branch, L. C., & Villarreal, D. (2011). Native herbivore exerts contrasting effects on fire regime and vegetation structure. *Oecologia*, *166*(4), 1121-1129.
51. Huntzinger, M., Karban, R., & Maron, J. L. (2011). Small mammals cause non-trophic effects on habitat and associated snails in a native system. *Oecologia*, *167*(4), 1085-1091.
52. Sosa, B., & Brazeiro, A. (2012). Local and landscape-scale effects of an ant nest construction in an open dry forest of Uruguay. *Ecological Entomology*, *37*(3), 252-255.
53. Erwin, D. H., & Tweedt, S. (2012). Ecological drivers of the Ediacaran-Cambrian diversification of Metazoa. *Evolutionary Ecology*, *26*(2), 417-433.
54. Jones, C. G. (2012). Ecosystem engineers and geomorphological signatures in landscapes. *Geomorphology*, *157*, 75-87.
55. DeVries, P. (2012). Salmonid influences on rivers: A geomorphic fish tail. *Geomorphology*, *157*, 66-74.
56. Huntsinger, L., Sayre, N. F., & Wulfhorst, J. D. (2012). Birds, beasts and bovines: three cases of pastoralism and wildlife in the USA. *Pastoralism: research, policy and practice*, *2*(1), 1-28.
57. Czarnecka, J., & Kitowski, I. (2013, January). The white stork as an engineering species and seed dispersal vector when nesting in Poland. In *Annales Botanici Fennici* (pp. 1-12). Finnish Zoological and Botanical Publishing Board.

58. Novoa, A., González, L., Moravcová, L., & Pyšek, P. (2013). Constraints to native plant species establishment in coastal dune communities invaded by Carpobrotus edulis: Implications for restoration. *Biological Conservation*, *164*, 1-9.
59. Nummi, P., & Kuuluvainen, T. (2013). Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes.
60. Ge, Z., Cao, H., & Zhang, L. (2013). A process-based grid model for the simulation of range expansion of Spartina alterniflora on the coastal saltmarshes in the Yangtze Estuary. *Ecological Engineering*, *58*, 105-112.
61. Lima, V. O., Demite, P. R., Vieira, C., Feres, R. J., & Romero, G. Q. (2013). Contrasting engineering effects of leaf-rolling caterpillars on a tropical mite community. *Ecological Entomology*, *38*(2), 193-200.
62. Meyer, S. T., Neubauer, M., Sayer, E. J., Leal, I. R., Tabarelli, M., & Wirth, R. (2013). Leaf-cutting ants as ecosystem engineers: topsoil and litter perturbations around Atta cephalotes nests reduce nutrient availability. *Ecological Entomology*, *38*(5), 497-504.
63. Bishop, M. J., Fraser, J., & Gribben, P. E. (2013). Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves. *Ecology*, *94*(9), 1927-1936.
64. Bryce, R., Van Der Wal, R., Mitchell, R., & Lambin, X. (2013). Metapopulation dynamics of a burrowing herbivore drive spatio-temporal dynamics of riparian plant communities. *Ecosystems*, *16*(7), 1165-1177.
65. Daryanto, S., Eldridge, D. J., & Wang, L. (2013). Spatial patterns of infiltration vary with disturbance in a shrub-encroached woodland. *Geomorphology*, *194*, 57-64.
66. Khaitov, V. (2013). Life in an unstable house: community dynamics in changing mussel beds. *Hydrobiologia*, *706*(1), 139-158.
67. Ebert, D., Hottinger, J. W., & Pajunen, V. I. (2013). Unsuitable habitat patches lead to severe underestimation of dynamics and gene flow in a zooplankton metapopulation. *Journal of animal ecology*, *82*(4), 759-769.
68. Sliwinski, M., & Sigmon, E. (2013). Why do leaf-tying caterpillars abandon their leaf ties?. *PeerJ*, *1*, e173.
69. Cameron, E. K., Proctor, H. C., & Bayne, E. M. (2013). Effects of an ecosystem engineer on belowground movement of microarthropods. *PLoS One*, *8*(4), e62796.
70. Dalbeck, L., Janssen, J., & Völsgen, S. L. (2014). Beavers (Castor fiber) increase habitat availability, heterogeneity and connectivity for common frogs (Rana temporaria). *Amphibia-Reptilia*, *35*(3), 321-329.
71. Fei, S., Phillips, J., & Shouse, M. (2014). Biogeomorphic impacts of invasive species. *Annual review of ecology, evolution, and systematics*, *45*, 69-87.
72. Anderson, C. B., Vanessa Lencinas, M., Wallem, P. K., Valenzuela, A. E., Simanonok, M. P., & Martinez Pastur, G. (2014). Engineering by an invasive species alters landscape-level ecosystem function, but does not affect biodiversity in freshwater systems. *Diversity and Distributions*, *20*(2), 214-222.
73. Corenblit, D., Steiger, J., González, E., Gurnell, A. M., Charrier, G., Darrozes, J., ... & Voldoire, O. (2014). The biogeomorphological life cycle of poplars during the fluvial biogeomorphological succession: a special focus on Populus nigra L. *Earth Surface Processes and Landforms*, *39*(4), 546-563.

74. Buser, C. C., Newcomb, R. D., Gaskett, A. C., & Goddard, M. R. (2014). Niche construction initiates the evolution of mutualistic interactions. *Ecology Letters*, *17*(10), 1257-1264.
75. Laland, K. N., Boogert, N., & Evans, C. (2014). Niche construction, innovation and complexity. *Environmental Innovation and Societal Transitions*, *11*, 71-86.
76. Hogg, R. S., Coghlan Jr, S. M., Zydlewski, J., & Simon, K. S. (2014). Anadromous sea lampreys (P etromyzon marinus) are ecosystem engineers in a spawning tributary. *Freshwater biology*, *59*(6), 1294-1307.
77. Donadi, S., van der Zee, E. M., van der Heide, T., Weerman, E. J., Piersma, T., van de Koppel, J., ... & Eriksson, B. K. (2014). The bivalve loop: intra-specific facilitation in burrowing cockles through habitat modification. *Journal of experimental marine biology and ecology*, *461*, 44-52.
78. Streitberger, M., Rose, S., Hermann, G., & Fartmann, T. (2014). The role of a mound-building ecosystem engineer for a grassland butterfly. *Journal of insect conservation*, *18*(4), 745-751.
79. Fraser, C. M., Coleman, R. A., & Seebacher, F. (2014). Trying to fit in: are patterns of orientation of a keystone grazer set by behavioural responses to ecosystem engineers or wave action?. *Oecologia*, *174*(1), 67-75.
80. Robles, H., & Martin, K. (2014). Habitat-mediated variation in the importance of ecosystem engineers for secondary cavity nesters in a nest web. *PLoS One*, *9*(2), e90071.
81. Włodarska-Kowalczuk, M., Jankowska, E., Kotwicki, L., & Balazy, P. (2014). Evidence of season-dependency in vegetation effects on macrofauna in temperate seagrass meadows (Baltic Sea). *PLoS One*, *9*(7), e100788.
82. Haupt, T. M., Sinclair, B. J., & Chown, S. L. (2014). Chemosensory and thermal cue responses in the sub-Antarctic moth Pringleophaga marioni: Do caterpillars choose Wandering Albatross nest proxies?. *Polar biology*, *37*(4), 555-563.
83. Zangerlé, A., Hissler, C., Blouin, M., & Lavelle, P. (2014). Near infrared spectroscopy (NIRS) to estimate earthworm cast age. *Soil Biology and Biochemistry*, *70*, 47-53.
84. Romero, G. Q., Gonçalves-Souza, T., Vieira, C., & Koricheva, J. (2015). Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*, *90*(3), 877-890.
85. Corenblit, D., Davies, N. S., Steiger, J., Gibling, M. R., & Bornette, G. (2015). Considering river structure and stability in the light of evolution: feedbacks between riparian vegetation and hydrogeomorphology. *Earth Surface Processes and Landforms*, *40*(2), 189-207.
86. Arkle, R. S., & Pilliod, D. S. (2015). Persistence at distributional edges: Columbia spotted frog habitat in the arid Great Basin, USA. *Ecology and evolution*, *5*(17), 3704-3724.
87. Tremblay, J. A., Savard, J. P. L., & Ibarzabal, J. (2015). Structural retention requirements for a key ecosystem engineer in conifer-dominated stands of a boreal managed landscape in eastern Canada. *Forest Ecology and Management*, *357*, 220-227.
88. Hood, G. A., & Larson, D. G. (2015). Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. *Freshwater Biology*, *60*(1), 198-208.
89. Corenblit, D., Baas, A., Balke, T., Bouma, T., Fromard, F., Garófano-Gómez, V., ... & Walcker, R. (2015). Engineer pioneer plants respond to and affect geomorphic

constraints similarly along water–terrestrial interfaces world-wide. *Global Ecology and Biogeography*, *24*(12), 1363-1376.

90. Colden, A. M., & Lipcius, R. N. (2015). Lethal and sublethal effects of sediment burial on the eastern oyster Crassostrea virginica. *Marine Ecology Progress Series*, *527*, 105-117.
91. Rabaoui, L., Belgacem, W., Ismail, D. B., Mansour, L., & Tlig-Zouari, S. (2015). Engineering effect of Pinna nobilis shells on benthic communities. *Oceanologia*, *57*(3), 271-279.
92. Simmons, W., Dávalos, A., & Blossey, B. (2015). Forest successional history and earthworm legacy affect earthworm survival and performance. *Pedobiologia*, *58*(4), 153-164.
93. Whitesides, C. J. (2015). The bioturbation of Olympic marmots (Marmota olympus) and their impacts on soil properties. *Physical Geography*, *36*(3), 202-214.
94. McCullough Hennessy, S., Deutschman, D. H., Shier, D. M., Nordstrom, L. A., Lenihan, C., Montagne, J. P., ... & Swaisgood, R. R. (2016). Experimental habitat restoration for conserved species using ecosystem engineers and vegetation management. *Animal Conservation*, *19*(6), 506-514.
95. Haupt, T. M., Sinclair, B. J., Shaw, J. D., & Chown, S. L. (2016). Further support for thermal ecosystem engineering by wandering albatross. *Antarctic Science*, *28*(1), 35-43.
96. Holm, M. W., Davids, J. K., Hansen, B. W., Dolmer, P., Holmes, E., Nielsen, T. T., & Vismann, B. (2016). Coexistence of Pacific oyster Crassostrea gigas (Thunberg, 1793) and blue mussels Mytilus edulis Linnaeus, 1758 on a sheltered intertidal bivalve bed?. *Aquatic Invasions*, *11*(2).
97. Bogusch, P., Macek, J., Janšta, P., Kubík, Š., Řezáč, M., Holý, K., ... & Heneberg, P. (2016). Industrial and post-industrial habitats serve as critical refugia for pioneer species of newly identified arthropod assemblages associated with reed galls. *Biodiversity and conservation*, *25*(5), 827-863.
98. Whitesides, C. J., & Butler, D. R. (2016). Bioturbation by gophers and marmots and its effects on conifer germination. *Earth Surface Processes and Landforms*, *41*(15), 2269-2281.
99. Phillips, J. D. (2016). Landforms as extended composite phenotypes. *Earth Surface Processes and Landforms*, *41*(1), 16-26.
100. Coverdale, T. C., Kartzinel, T. R., Grabowski, K. L., Shriver, R. K., Hassan, A. A., Goheen, J. R., ... & Pringle, R. M. (2016). Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. *Ecology*, *97*(11), 3219-3230.
101. Laland, K., Matthews, B., & Feldman, M. W. (2016). An introduction to niche construction theory. *Evolutionary ecology*, *30*(2), 191-202.
102. Walles, B., Smaal, A. C., Herman, P. M., & Ysebaert, T. (2016). Niche dimension differs among life-history stages of Pacific oysters in intertidal environments. *Marine Ecology Progress Series*, *562*, 113-122.
103. Cornelissen, T., Cintra, F., & Santos, J. C. (2016). Shelter-building insects and their role as ecosystem engineers. *Neotropical entomology*, *45*(1), 1-12.
104. Bordy, E. M., & Krummeck, W. D. (2016). Enigmatic continental burrows from the Early Triassic transition of the Katberg and Burgersdorp formations in the main Karoo Basin, South Africa. *Palaios*, *31*(8), 389-403.

105. Melguizo-Ruiz, N., Jiménez-Navarro, G., & Moya-Laraño, J. (2016). Beech cupules as keystone structures for soil fauna. *PeerJ*, *4*, e2562.
106. Phillips, J. D. (2016). Biogeomorphology and contingent ecosystem engineering in karst landscapes. *Progress in Physical Geography*, *40*(4), 503-526.
107. Schweiger, A. H., & Beierkuhnlein, C. (2017). The ecological legacy of 20th century acidification carried on by ecosystem engineers. *Applied Vegetation Science*, *20*(2), 215-224.
108. Valentine, L. E., Bretz, M., Ruthrof, K. X., Fisher, R., Hardy, G. E. S. J., & Fleming, P. A. (2017). Scratching beneath the surface: Bandicoot bioturbation contributes to ecosystem processes. *Austral Ecology*, *42*(3), 265-276.
109. Novais, S. M., DaRocha, W. D., Calderon-Cortes, N., & Quesada, M. (2017). Wood-boring beetles promote ant nest cavities: extended effects of a twig-girdler ecosystem engineer. *Basic and Applied Ecology*, *24*, 53-59.
110. Kui, L., Stella, J. C., Shafroth, P. B., House, P. K., & Wilcox, A. C. (2017). The long-term legacy of geomorphic and riparian vegetation feedbacks on the dammed Bill Williams River, Arizona, USA. *Ecohydrology*, *10*(4), e1839.
111. Howison, R. A., Olff, H., van de Koppel, J., & Smit, C. (2017). Biotically driven vegetation mosaics in grazing ecosystems: the battle between bioturbation and biocompaction. *Ecological Monographs*, *87*(3), 363-378.
112. Reynolds, P. L., Glanz, J., Yang, S., Hann, C., Couture, J., & Grosholz, E. (2017). Ghost of invasion past: legacy effects on community disassembly following eradication of an invasive ecosystem engineer. *Ecosphere*, *8*(3), e01711.
113. Alves, R. M., Vanaverbeke, J., Bouma, T. J., Guarini, J. M., Vincx, M., & Van Colen, C. (2017). Effects of temporal fluctuation in population processes of intertidal Lanice conchilega (Pallas, 1766) aggregations on its ecosystem engineering. *Estuarine, Coastal and Shelf Science*, *188*, 88-98.
114. Koza, A., Kuśmierska, A., McLaughlin, K., Moshynets, O., & Spiers, A. J. (2017). Adaptive radiation of Pseudomonas fluorescens SBW25 in experimental microcosms provides an understanding of the evolutionary ecology and molecular biology of AL interface biofilm formation. *FEMS microbiology letters*, *364*(12).
115. Šklíba, J., Vlasata, T., Lövy, M., Hrouzkova, E., Meheretu, Y., Sillero-Zubiri, C., & Šumbera, R. (2017). Ecological role of the giant root-rat (Tachyoryctes macrocephalus) in the Afroalpine ecosystem. *Integrative zoology*, *12*(4), 333-344.
116. Dias, A. T. C., Cornelissen, J. H., & Berg, M. P. (2017). Litter for life: assessing the multifunctional legacy of plant traits. *Journal of Ecology*, *105*(5), 1163-1168.
117. Alves, R. M., Van Colen, C., Vincx, M., Vanaverbeke, J., De Smet, B., Guarini, J. M., ... & Bouma, T. J. (2017). A case study on the growth of Lanice conchilega (Pallas, 1766) aggregations and their ecosystem engineering impact on sedimentary processes. *Journal of Experimental Marine Biology and Ecology*, *489*, 15-23.
118. Aya-Cuero, C., Rodríguez-Bolaños, A., & Superina, M. (2017). Population density, activity patterns, and ecological importance of giant armadillos (Priodontes maximus) in Colombia. *Journal of Mammalogy*, *98*(3), 770-778.
119. Barbier, P., Meziane, T., Forêt, M., Tremblay, R., Robert, R., & Olivier, F. (2017). Nursery function of coastal temperate benthic habitats: New insight from the bivalve recruitment perspective. *Journal of Sea Research*, *121*, 11-23.

120. Reise, K., Buschbaum, C., Büttger, H., Rick, J., & Wegner, K. M. (2017). Invasion trajectory of Pacific oysters in the northern Wadden Sea. *Marine biology*, *164*(4), 68.
121. Powers, S. P., Rouhani, S., Baker, M. C., Roman, H., Grabowski, J. H., Scyphers, S. B., ... & Hester, M. W. (2017). Ecosystem services are lost when facilitation between two ecosystem engineers is compromised by oil. *Marine Ecology Progress Series*, *576*, 189-202.
122. Colden, A. M., Latour, R. J., & Lipcius, R. N. (2017). Reef height drives threshold dynamics of restored oyster reefs. *Marine Ecology Progress Series*, *582*, 1-13.
123. Ballinger, M. J., Moore, L. D., & Perlman, S. J. (2018). Evolution and diversity of inherited Spiroplasma symbionts in Myrmica ants. *Applied and Environmental Microbiology*, *84*(4), e02299-17.
124. Harvey, G. L., Henshaw, A. J., Parker, C., & Sayer, C. D. (2018). Re-introduction of structurally complex wood jams promotes channel and habitat recovery from overwidening: Implications for river conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*(2), 395-407.
125. Moore, J. L., Puckett, B. J., & Schreiber, S. J. (2018). Restoration of eastern oyster populations with positive density dependence. *Ecological applications*, *28*(4), 897-909.
126. Haussmann, N. S., Louw, M. A., Lewis, S., Nicol, K. J., Van der Merwe, S., & le Roux, P. C. (2018). Ecosystem engineering through aardvark (Orycteropus afer) burrowing: Mechanisms and effects. *Ecological Engineering*, *118*, 66-72.
127. Nickell, Z., Varriano, S., Plemmons, E., & Moran, M. D. (2018). Ecosystem engineering by bison (Bison bison) wallowing increases arthropod community heterogeneity in space and time. *Ecosphere*, *9*(9), e02436.
128. Mudrák, O., & Frouz, J. (2018). Earthworms increase plant biomass more in soil with no earthworm legacy than in earthworm-mediated soil, and favour late successional species in competition. *Functional Ecology*, *32*(3), 626-635.
129. Corenblit, D., Garófano-Gómez, V., González, E., Hortobágyi, B., Julien, F., Lambs, L., ... & Till-Bottraud, I. (2018). Niche construction within riparian corridors. Part II: The unexplored role of positive intraspecific interactions in Salicaceae species. *Geomorphology*, *305*, 112-122.
130. Atkinson, C. L., Allen, D. C., Davis, L., & Nickerson, Z. L. (2018). Incorporating ecogeomorphic feedbacks to better understand resiliency in streams: a review and directions forward. *Geomorphology*, *305*, 123-140.
131. Grinath, J. B., Deguines, N., Chesnut, J. W., Prugh, L. R., Brashares, J. S., & Suding, K. N. (2018). Animals alter precipitation legacies: Trophic and ecosystem engineering effects on plant community temporal dynamics. *Journal of Ecology*, *106*(4), 1454-1469.
132. Commito, J. A., Jones, B. R., Jones, M. A., Winders, S. E., & Como, S. (2018). What happens after mussels die? Biogenic legacy effects on community structure and ecosystem processes. *Journal of Experimental Marine Biology and Ecology*, *506*, 30-41.
133. Novais, S., Calderón-Cortés, N., Sánchez-Montoya, G., & Quesada, M. (2018). Arthropod facilitation by wood-boring beetles: spatio-temporal distribution mediated by a twig-girdler ecosystem engineer. *Journal of Insect Science*, *18*(5), 14.
134. Joseph, G. S., Seymour, C. L., Coetzee, B. W., Ndlovu, M., Deng, L., Fowler, K., ... & Foord, S. H. (2018). Elephants, termites and mound thermoregulation in a progressively warmer world. *Landscape ecology*, *33*(5), 731-742.

135. Martin, J., Vourc'h, G., Bonnot, N., Cargnelutti, B., Chaval, Y., Lourtet, B., ... & Morellet, N. (2018). Temporal shifts in landscape connectivity for an ecosystem engineer, the roe deer, across a multiple-use landscape. *Landscape ecology*, *33*(6), 937-954.
136. Mukherjee, A., Kumara, H. N., & Bhupathy, S. (2018). Environmental determinants of activity variation of an overlooked burrowing rodent: the Indian crested porcupine. *Mammalia*, *82*(5), 449-459.
137. 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*(1), 251-262.
138. Costa, A. N., Bruna, E. M., & Vasconcelos, H. L. (2018). Do an ecosystem engineer and environmental gradient act independently or in concert to shape juvenile plant communities? Tests with the leaf-cutter ant Atta laevigata in a Neotropical savanna. *PeerJ*, *6*, e5612.
139. Willby, N. J., Law, A., Levanoni, O., Foster, G., & Ecke, F. (2018). Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761), 20170444.
140. Polvi, L. E., & Sarneel, J. M. (2018). Ecosystem engineers in rivers: An introduction to how and where organisms create positive biogeomorphic feedbacks. *Wiley Interdisciplinary Reviews: Water*, *5*(2), e1271.
141. Prazeres, M., & Renema, W. (2019). Evolutionary significance of the microbial assemblages of large benthic Foraminifera. *Biological Reviews*, *94*(3), 828-848.
142. Commito, J. A., Jones, B. R., Jones, M. A., Winders, S. E., & Como, S. (2019). After the fall: Legacy effects of biogenic structure on wind-generated ecosystem processes following mussel bed collapse. *Diversity*, *11*(1), 11.
143. Grenfell, M. C., Aalto, R., Grenfell, S. E., & Ellery, W. N. (2019). Ecosystem engineering by hummock-building earthworms in seasonal wetlands of eastern South Africa: insights into the mechanics of biomorphodynamic feedbacks in wetland ecosystems. *Earth Surface Processes and Landforms*, *44*(1), 354-366.
144. Laurel, D., & Wohl, E. (2019). The persistence of beaver-induced geomorphic heterogeneity and organic carbon stock in river corridors. *Earth Surface Processes and Landforms*, *44*(1), 342-353.
145. Norby, R. J., Childs, J., Hanson, P. J., & Warren, J. M. (2019). Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. *Ecology and Evolution*, *9*(22), 12571-12585.
146. Tumolo, B. B., Albertson, L. K., Cross, W. F., Daniels, M. D., & Sklar, L. S. (2019). Occupied and abandoned structures from ecosystem engineering differentially facilitate stream com
147. Bush, B. M., Stenert, C., Maltchik, L., & Batzer, D. P. (2019). Beaver-created successional gradients increase β-diversity of invertebrates by turnover in stream-wetland complexes. *Freshwater Biology*, *64*(7), 1265-1274.
148. Barbosa, M., Fernandes, G. W., & Morris, R. J. (2019). Interaction engineering: Non-trophic effects modify interactions in an insect galler community. *Journal of Animal Ecology*, *88*(8), 1168-1177.

149. Campos, H., Boeing, W. J., & Throop, H. L. (2019). Decaying woodrat (Neotoma spp.) middens increase soil resources and accelerate decomposition of contemporary litter. *Journal of Arid Environments*, *171*, 104007.

150. McAuliffe, J. R., Hoffman, M. T., McFadden, L. D., Jack, S., Bell, W., & King, M. P. (2019). Whether or not heuweltjies: Context-dependent ecosystem engineering by the southern harvester termite, Microhodotermes viator. *Journal of Arid Environments*, *163*, 26-33.

151. Rengifo-Faiffer, M. C., & Arana, C. (2019). Fossorial birds help shape the plant community of a Peruvian desert. *Journal of Arid Environments*, *169*, 29-33.

152. Mourya, N. R., Bargali, K., & Bargali, S. S. (2019). Impacts of Coriaria nepalensis colonization on vegetation structure and regeneration dynamics in a mixed conifer forest of Indian Central Himalaya. *Journal of Forestry Research*, *30*(1), 305-317.

153. Fernandez-Bou, A. S., Dierick, D., Swanson, A. C., Allen, M. F., Alvarado, A. G. F., Artavia-León, A., ... & Harmon, T. C. (2019). The role of the ecosystem engineer, the leaf-cutter ant Atta cephalotes, on soil CO2 dynamics in a wet tropical rainforest. *Journal of Geophysical Research: Biogeosciences*, *124*(2), 260-273.

154. Dawson, S. J., Broussard, L., Adams, P. J., Moseby, K. E., Waddington, K. I., Kobryn, H. T., ... & Fleming, P. A. (2019). An outback oasis: the ecological importance of bilby burrows. *Journal of Zoology*, *308*(3), 149-163.

155. Barry, J. M., Elbroch, L. M., Aiello-Lammens, M. E., Sarno, R. J., Seelye, L., Kusler, A., ... & Grigione, M. M. (2019). Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem. *Oecologia*, *189*(3), 577-586.

156. Massé Jodoin, J., & Guichard, F. (2019). Non-resource effects of foundation species on meta-ecosystem stability and function. *Oikos*, *128*(11), 1613-1632.

157. Ilarri, M. I., Souza, A. T., Amorim, L., & Sousa, R. (2019). Decay and persistence of empty bivalve shells in a temperate riverine system. *Science of the Total Environment*, *683*, 185-192.

158. Levine, R., & Meyer, G. A. (2019). Beaver-generated disturbance extends beyond active dam sites to enhance stream morphodynamics and riparian plant recruitment. *Scientific reports*, *9*(1), 1-12.

159. Zbyryt, A., Sparks, T. H., & Tryjanowski, P. (2020). Foraging efficiency of white stork Ciconia ciconia significantly increases in pastures containing cows. *Acta Oecologica*, *104*, 103544.

160. Lavelle, P., Spain, A., Fonte, S., Bedano, J. C., Blanchart, E., Galindo, V., ... & Zangerlé, A. (2020). Soil aggregation, ecosystem engineers and the C cycle. *Acta Oecologica*, *105*, 103561.

161. Weinersmith, K. L., Forbes, A. A., Ward, A. K., Brandão-Dias, P. F., Zhang, Y. M., & Egan, S. P. (2020). Arthropod Community Associated With the Asexual Generation of Bassettia pallida (Hymenoptera: Cynipidae). *Annals of the Entomological Society of America*, *113*(5), 373-388.

162. Clayton, J., Gardner, M. G., Fenner, A. L., & Bull, M. (2020). Co-occupancy of spider-engineered burrows within a grassland community changes temporally. *Austral Ecology*, *45*(4), 454-459.

163. Ross, C. E., McIntyre, S., Barton, P. S., Evans, M. J., Cunningham, S. A., & Manning, A. D. (2020). A reintroduced ecosystem engineer provides a germination niche for native plant species. *Biodiversity and Conservation*, *29*(3), 817-837.

164. Hood, G. A. (2020). Not all ponds are created equal: long-term beaver (Castor canadensis) lodge occupancy in a heterogeneous landscape. *Canadian Journal of Zoology*, *98*(3), 210-218.
165. Gutiérrez, J. L. (2020). Ecosystem Engineers in the World Coasts: Case Studies and Conceptual Linkages. *Diversity*, *12*(6), 243.
166. Hafen, K. C., Wheaton, J. M., Roper, B. B., Bailey, P., & Bouwes, N. (2020). Influence of topographic, geomorphic, and hydrologic variables on beaver dam height and persistence in the intermountain western United States. *Earth Surface Processes and Landforms*, *45*(11), 2664-2674.
167. Jabłońska, E., Michaelis, D., Tokarska, M., Goldstein, K., Grygoruk, M., Wilk, M., ... & Kotowski, W. (2020). Alleviation of plant stress precedes termination of rich fen stages in peat profiles of lowland mires. *Ecosystems*, *23*(4), 730-740.
168. Kivinen, S., Nummi, P., & Kumpula, T. (2020). Beaver-induced spatiotemporal patch dynamics affect landscape-level environmental heterogeneity. *Environmental Research Letters*, *15*(9), 094065.
169. Maguire, Z., Tumolo, B. B., & Albertson, L. K. (2020). Retreat but no surrender: net-spinning caddisfly (Hydropsychidae) silk has enduring effects on stream channel hydraulics. *Hydrobiologia*, *847*(6), 1539-1551.
170. Becker, B. J., Behrens, M. D., Allen, B., Hintz, M., Parker, H., McCartha, M. M., & White, S. M. (2020). Spatial and temporal distribution of the early life history stages of the native Olympia oyster Ostrea lurida (Carpenter, 1864) in a restoration site in northern Puget Sound, WA. *Journal of Shellfish Research*, *39*(1), 43-58.
171. Booth, M. T., Hairston Jr, N. G., & Flecker, A. S. (2020). Consumer movement dynamics as hidden drivers of stream habitat structure: Suckers as ecosystem engineers on the night shift. *Oikos*, *129*(2), 194-208.
172. Novais, S., Aguirre-Jaimes, A., Quesada, M., & Hernández-Ortiz, V. (2020). Ecosystem engineering by leaf-rolling mites enhances arthropod diversity. *The Science of Nature*, *107*(5), 1-6.
173. Cribb, A. T., & Bottjer, D. J. (2020). Complex marine bioturbation ecosystem engineering behaviors persisted in the wake of the end-Permian mass extinction. *Scientific reports*, *10*(1), 1-8.
174. Dohner, S. M., Stockwell, C. L., Miller, D. C., & Trembanis, A. C. (2020). Characterization of worm reefs (Sabellaria vulgaris) in Delaware Bay, United States. In *Seafloor geomorphology as benthic habitat* (pp. 163-174). Elsevier.

Tables

Table 1. Definitions of terminology.

Term	**Definition**	**References** Seminal; case study example
Ecosystem engineer	Organisms that create, maintain, or modify physical habitat or resource flows . These effects feedback on the organism itself (a kind of niche construction) but also transform entire local ecosystems that other organisms experience. Commonly recognized examples include corals, beavers, and burrowing activities of, for example, earthworms (terrestrial) or polychaetes (marine).	Jones et al., 1994; Messmer et al., 2011
Extended phenotype	Phenotypes of organisms that project beyond their surfaces into the surrounding environment. Extended phenotypes often are built structures, like nests, burrows, and dams, and they represent a kind of artifact arising from physiological or behavioral processes of the builder.	Dawkins, 1982; Edwards et al., 2020
Ecosystem engineering legacy	Transformations of the environment that persist beyond the disappearance or death of the transforming organisms and that affect other organisms in the community. The legacy can be physical, biological, or chemical.	Hastings et al., 2007; Johnson-Bice et. al., 2022
Niche construction	Activities or structures of organisms that influence the biotic or abiotic environments that they experience. Leaf-mining insects, for example, can raise or lower the temperatures that they experience by altering local leaf radiative and evaporative budgets. In turn, such altered environments can shape evolutionary pressures on, for example, critical thermal maxima.	Odling-Smee et al., 1996; Pincebourde & Casas, 2019

Table 2.

Examples of ecosystem engineers and their legacies drawn from the studies identified by the literature search. The examples provided here were selected by the authors as an illustrative subset of the 174 studies (Appendix A). Taxa are arranged in alphabetical order. The symbol ↟ in the Taxon column identifies autogenic engineers; no symbol identifies allogenic engineers. Abbreviations are: m = meter; ND = non-dimensional; Repro. = reproduction; yr = year.

Table 2A: Individual Ecosystem Engineers

Taxon	Latin name	Body size (m)	Lifespan (yr)	Modification	Purpose	Structure size (m)	Occupation time (yr)	Decay time (yr)	Frequency	ND Spatial	ND Temporal	Citation
Albatross	*Diomedea exulans*	1	50	Nest	Reproduction	1	0.19	1	Bi-annual	1	5.3	Haupt et al., (2016)
Bandicoot	*Isoodon fuscivente*r	0.5	3	Pit	Food	0.1	0.0027	0.5	Daily	0.2	183	Valentine et al., (2018)
Bettong	*Bettongia lesueur*	0.35	5	Pit	Food	0.1	0.0027	1	Daily	0.29	365	Ross et al., (2020)
Bilby	*Macrotis lagotis*	0.55	7	Pit	Food/shelter	2	1.15	30	Daily	3.6	26	Dawson et al., (2019)
Bison	*Bison latifrons*	2.5	10	Wallow	Cleaning	4	1	125	Multiple	1.6	125	Nickell et al., (2018)
Caddisfly	Hydropsychidae	0.02	1	Net	Food	0.02	0.083	0.17	Monthly	1	2	Tumolo et al., (2019)
Echidna	*Tachyglossus aculeatus*	0.3	50	Pit	Reproduction	0.2	0.55	1.5	Annual	0.67	2.7	Eldridge & Koen, (2021)
Eider duck	*Somateria mollissima*	0.5	20	Fecal matter	Waste	5	0.25	1	Seasonal	10	4	Ebert et al., (2013)
Elephant	*Loxodonta africana*	4	60	Tree removal	Food	60	1	7	Seasonal	15	7	Pringle, (2008)
Kangaroo rat	*Dipodomys spectabilis*	0.3	3	Burrow	Shelter	5	3	70	Lifetime	17	23	Guo, (1996)
Lamprey	*Petromyzon marinus*	1	4	Redd	Repro.	1	0.42	0.25	Lifetime	1	0.6	Hogg et al., (2014)
Moth	*Pseudoltephusa* sp.	0.01	1	Leaf tie	Pupation	0.05	0.038	0.33	Lifetime	5	8.5	Lill & Marquis, (2003)
Puma	*Puma concolor*	2	8	Carcass	Food	1	0.019	0.12	Monthly	0.5	6.3	Barry et al., (2019)
Rabbit	*Oryctolagus cuniculus*	0.4	9	Pit	Breeding	0.1	0.1	2	Daily	0.25	20	James et al., (2011)
Salmon	*Oncorhynchus* sp.	1	5	Redd	Reproduction	0.5	0.02	1	Lifetime	0.5	50	Verspoor et al., (2010)
Shrub	*Noaea mucronata*	1	5	Soil chemistry	Growth	2	5	5	Lifetime	2	1	Stavi et al., (2021)
Stingray	Dasyatidae	2	15	Pit	Food	0.5	0.0027	0.01	Daily	0.25	3.7	D'Andrea et al., (2002)
Sunfish	Centrachidae	0.13	3	Pit	Reproduction	1.2	0.083	1	Annual	9.2	12	Thorp, (1988)
Vole	*Microtus californicus*	0.15	0.5	Plant removal	Food	0.5	0.5	7	Daily	3.3	14	Huntzinger et al., (2011)
Woodpecker	*Dendrocopos major*	0.2	5	Tree hole	Nesting	0.3	0.083	50	Yearly	1.5	600	Catalina-Allueva & Martin,
Worm	Multiple	0.1	1	Cast	Waste	0.05	0.17	1	Daily	0.5	6	Zangerlé et al., (2014)

Table 2B: Conspecific Ecosystem Engineers

Taxon	Latin name	Body Size (m)	Lifespan (yr)	Abundance	Modification	Purpose	Structure size	Decay time (yr)	ND Temporal	ND Spatial	Citation
Beaver	*Castor Canadensis*	0.5	10	3/dam	Dam	Habitat, food	100 m	100	10	67	Bush et al., (2019)
Biofilms	Multiple	10^{-6}	0.001	$10^{-12}/m^2$	Binding sediment	Growth	1 m^2	0.003	3	1	Friend et al., (2003)
Blue mussel[†]	*Mytilus edulis*	0.1	10	$25/m^2$	Reefs	Food	50 m^2	30	3	2	Commito et al., (2019)

Coral↟	Multiple	0.01	10	750,000/m^2	Reef	Habitat	5,000 m^2	10^6	10^5	0.12	Jackson-Bue´ et al., (2021)
Cordgrass↟	*Spartina*	0.3	5	50/m^2	Sediment trap	Growth	1 m^2	4	3.3	0.47	Smith et al., (2018)
Eastern oyster↟	*Crassostrea virginica*	0.04	5	3,000/m^2	Multiple effects	Food	120,000 m^2	10	2	0.46	Reise et al., (2017)
Freshwater mussel↟	Multiple	0.06	5	20/m^2	Multiple effects	Food	1 m^2	5	1	3.7	Ilarri et al., (2019)
Ground-creeping plant	*Carpobrotus edulis*	0.1	20	20/m^2	Soil chemistry	Growth	0.5 m^2	1	0.05	2.2	Novoa et al., (2013)
Leaf-cutting ant	*Atta* sp.	0.002	0.2	10^6/mound	Mounds	Shelter	70 m^2	2	10	4.2	Costa et al., (2018)
Mite	*Calacarus flagelliseta*	10^{-4}	1	10^4/leaf	Leaf tie	Repro.	0.4 m^2	0.5	0.5	63	Fournier et al., (2003)
Poplar↟	*Populus nigra*	10	50	0.4/m	Sediment trap	Growth	25 m	40	0.8	0.25	Corenblit et al., (2014)
Termites	Multiple	0.01	1	10^6/mound	Mounds	Shelter	200 m^2	4,000	4,000	1.4	Joseph et al., (2018)
Vizcacha	*Lagostomus maximus*	0.3	10	15/pile	Litter pile	Food	5 m	5	0.5	1.1	Hierro et al., (2011)

Table 2C: Ecosystem Engineer Collectives

Soils of mountains of Luquillo National Forest, Puerto Rico; Thickness = 1 m; Soil production rate = 0.1 m/1000 yrs; Decay time = 10,000 years

Taxon	**Latin name**	**Body size (m)**	**Lifespan (yr)**	**Modification**	**Abundance**	**Citation**
Bacteria	*Cupriavidus* sp.	10^{-6}	10^{-6}	Iron oxidation, mineral weathering	10^8/g	Napieralski et al., (2019)
Worm	*Pontoscolex corethrurus*	0.1	0.1	Soil bioturbation, cast generation	90/m^2	Lavelle, (2007)
Tabonuco	*Dacryodes excelsa*	30	75	Rock fracture, soil bioturbation	200/ha	Scatena & Lugo, (1995)

Travertine dams and pools of Fossil Creek, Arizona; height = 3 m; growth rate = 0.01 m/yr; Decay time = 300 years

Taxon	**Latin name**	**Body size (m)**	**Lifespan (yr)**	**Modification**	**Abundance**	**Citation**
Cyanobacteria	*Synechococcus*	10^{-6}	0.3	Raise pH	10^7/m^2	Takashima & Kano, (2008)
Water silk↟	*Spirogyra*	0.01	0.3	Surface for CaCO3 precipitation	10^6/m^2	Compson et al., (2009)
Cottonwood↟	*Populus fremontii*	10	50	Blocking water flow	100/ha	Viles & Pentecost, (1999)

Figure Legends

Figure 1. (A) Ecosystem engineering organisms can leave legacies that range from small (green) to large (blue) duration (A) and spatial extent (B), and from low (green) to high (blue) frequency through time (C) and through space (D). These three attributes – duration, spatial extent, and frequency – of the modification contribute to the magnitude of the legacy.

Figure 2. Summary of ecosystem engineering papers studying legacy effects from 1994 to 2020; see Appendix A for additional information. (A) The number of papers studying legacy effects through time. Black circles show all papers identified by any of the search terms in panel A and gray circles show those papers identified using only the specific search term “legac*.” (B) The number of papers identified by each search term, ordered from highest to lowest. There were 28 papers that matched with more than one of the search terms.

Figure 3. Duration of an engineered structure through time and its spatial extent determine legacy magnitude. Living strategies such as individuals (purple) or groups of organisms (orange) and collective actions of multiple organisms (grey), provide additional context for understanding ecosystem engineering legacies.

Figure 4. Non-dimensional framework for evaluating the strength of ecosystem engineering legacy effects. (A) Ecosystem engineering examples that illustrate the wide range of legacies documented in the literature, scaled by lifespan and body size of the engineer. Legacy effect is a function of structure duration (temporal extent relative to time of engineer occupation) and size

(spatial extent relative to engineer body size). Living strategies of the engineer(s) may influence the relative importance of spatial versus temporal extent, as suggested by the differences in plotting positions of single individuals (purple) and conspecific groups (orange). We categorized each example as individual or group by taking cues from the language used by the author(s) of the original paper when the information was not explicitly stated; see Table 2 and Appendix A for additional information. (B) A general framework for relating legacy magnitude to the lifespan and body size of the engineer doing the work. Legacies fall along a gradient, where those that last as long or longer or are as large or larger than the engineer are stronger (blue), and those that are relatively brief or small are weaker (green) or negligible (grey).

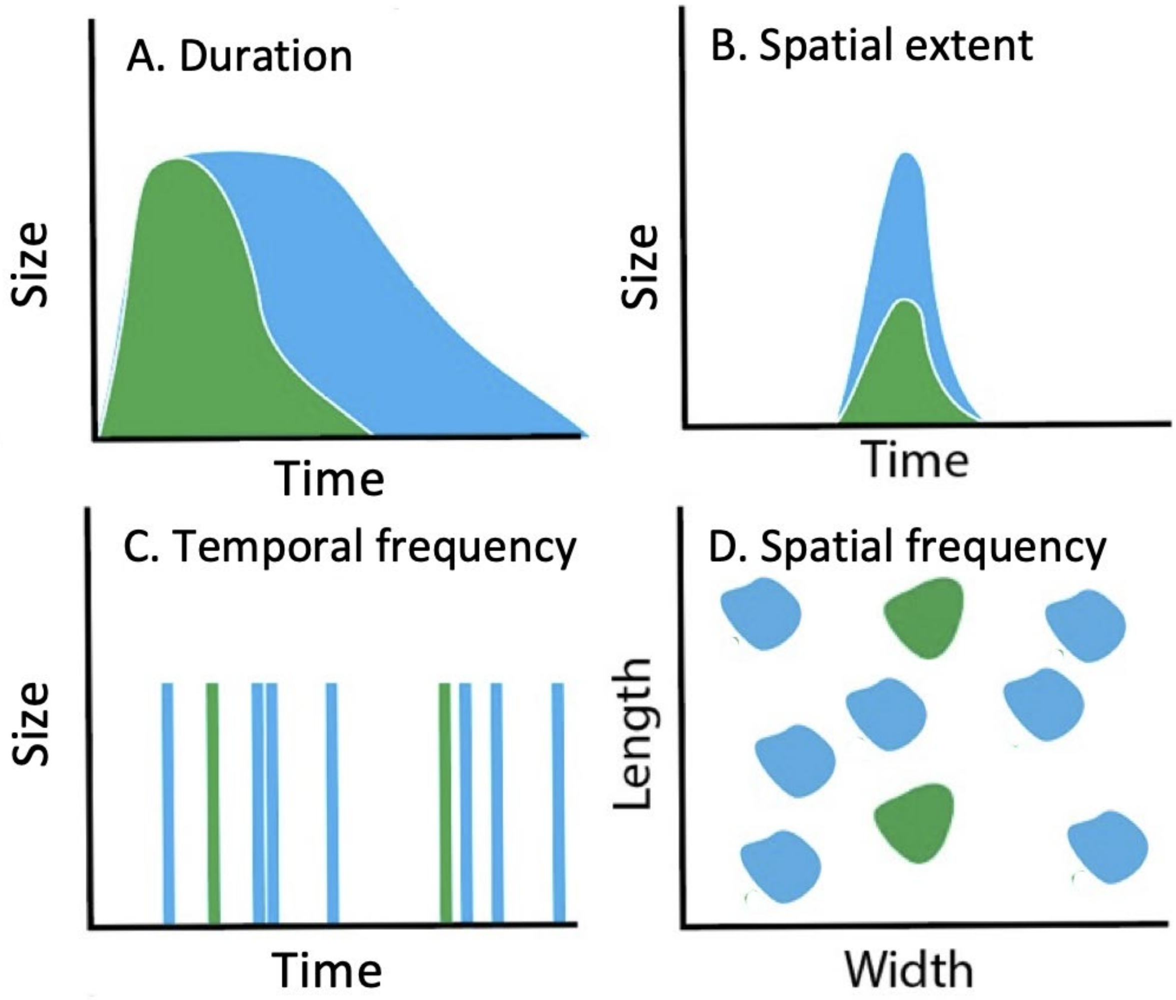
A. Duration
Size
Time
B. Spatial extent
Size
Time
C. Temporal frequency
Size
Time
D. Spatial frequency
Length
Width

Figure 1.

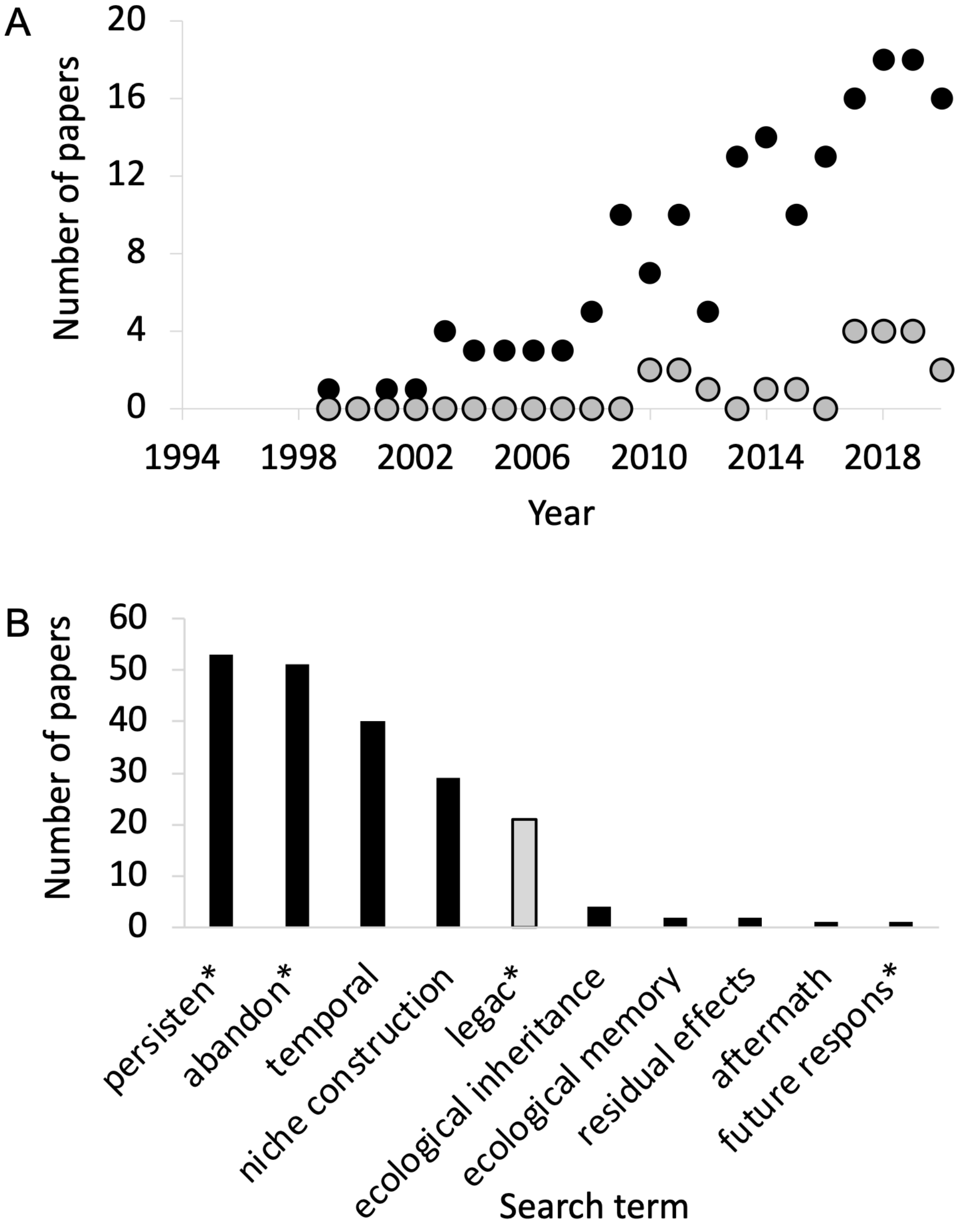
A
Number of papers
20
16
12
8
4
0
1994
1998
2002
2006
2010
2014
2018
Year
B
Number of papers
60
50
40
30
20
10
0
persisten*
abandon*
temporal
niche construction
legac*
ecological inheritance
ecological memory
residual effects
aftermath
future respons*
Search term

Figure 2.

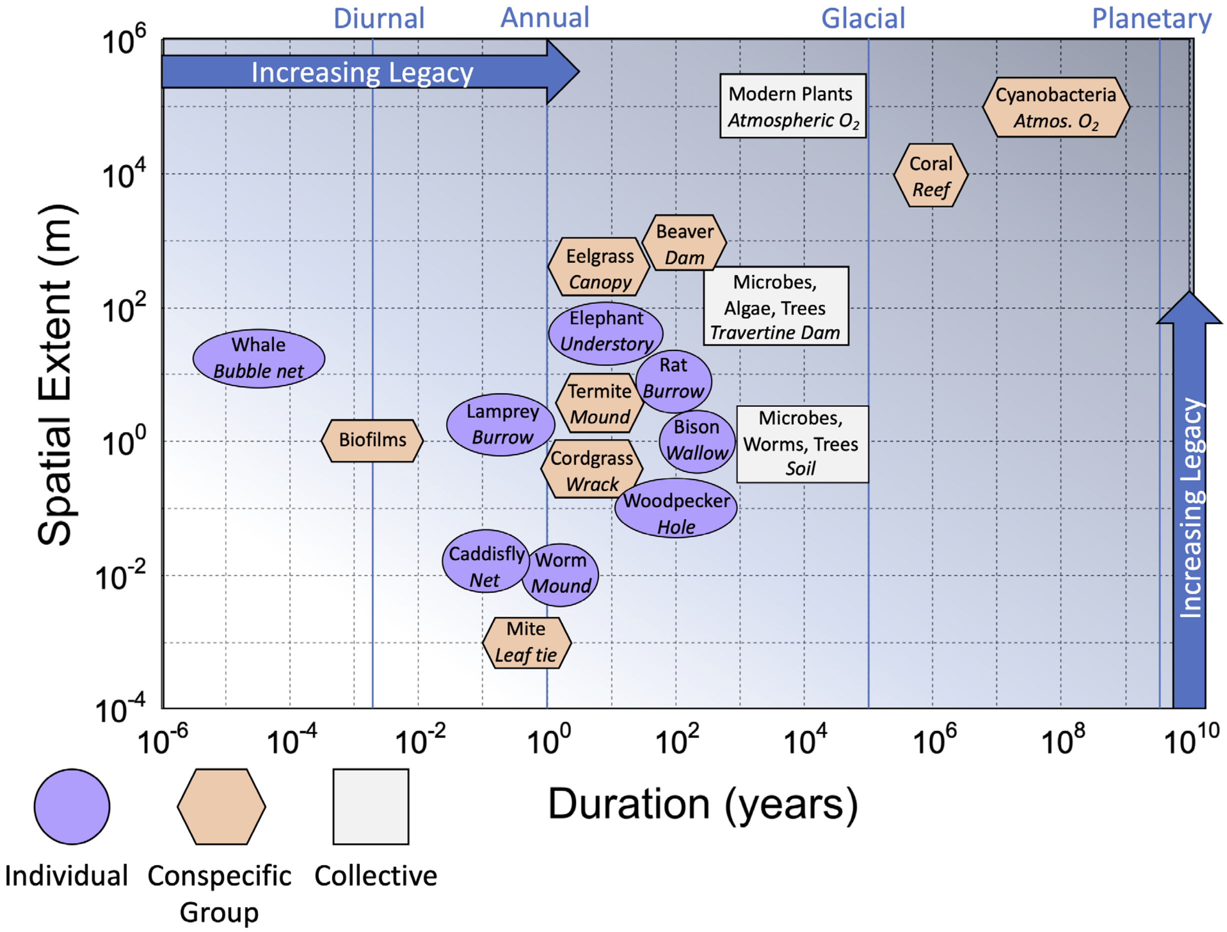
Diurnal
Annual
Glacial
Planetary
Increasing Legacy
Modern Plants
Atmospheric O_2
Cyanobacteria
Atmos. O_2
Coral
Reef
Beaver
Dam
Eelgrass
Canopy
Microbes,
Algae, Trees
Travertine Dam
Elephant
Understory
Whale
Bubble net
Rat
Burrow
Termite
Mound
Lamprey
Burrow
Biofilms
Bison
Wallow
Microbes,
Worms, Trees
Soil
Cordgrass
Wrack
Woodpecker
Hole
Caddisfly
Net
Worm
Mound
Mite
Leaf tie
Increasing Legacy
Spatial Extent (m)
10^6
10^4
10^2
10^0
10^{-2}
10^{-4}
10^{-6}
10^{-4}
10^{-2}
10^0
10^2
10^4
10^6
10^8
10^{10}
Duration (years)
Individual
Conspecific Group
Collective

Figure 3.

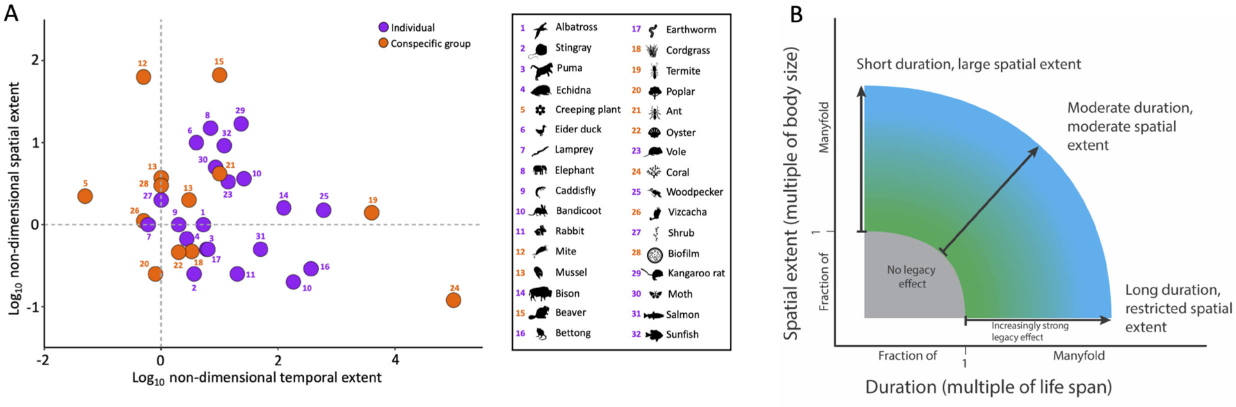
A
Individual
Conspecific group
Log10 non-dimensional spatial extent
Log10 non-dimensional temporal extent
-2
0
2
4
-1
0
1
2
1 Albatross
2 Stingray
3 Puma
4 Echidna
5 Creeping plant
6 Eider duck
7 Lamprey
8 Elephant
9 Caddisfly
10 Bandicoot
11 Rabbit
12 Mite
13 Mussel
14 Bison
15 Beaver
16 Bettong
17 Earthworm
18 Cordgrass
19 Termite
20 Poplar
21 Ant
22 Oyster
23 Vole
24 Coral
25 Woodpecker
26 Vizcacha
27 Shrub
28 Biofilm
29 Kangaroo rat
30 Moth
31 Salmon
32 Sunfish
B
Short duration, large spatial extent
Moderate duration, moderate spatial extent
Long duration, restricted spatial extent
No legacy effect
Increasingly strong legacy effect
Spatial extent (multiple of body size)
Manyfold
1
Fraction of
Duration (multiple of life span)
Fraction of
1
Manyfold

Figure 4.