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REVIEW

Ecosystem Engineers: Cross-scale and Cross-system Perspectives

The ghosts of ecosystem engineers: Legacy effects of biogenic modifications

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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, life span 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 such as 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

TABLE 1 Definitions of terminology

Term	Definition	Germinal citation; 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 behavioural 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

(a): Individual ecosystem engineers

Taxon	Latin name	Body size (m)	Life span (year)	Modification	Purpose	Structure size (m)	Occupation time (year)	Decay time (year)	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 fusciventer*	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 and Koen (2021)
Eider duck	*Somateria mollissima*	0.5	20	Faecal 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 and 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 and Martín (2021)
Worm	Multiple	0.1	1	Cast	Waste	0.05	0.17	1	Daily	0.5	6	Zangerlé et al. (2014)

TABLE 2 (Continued)

(b): Conspecific ecosystem engineers											
Taxon	Latin name	Body size (m)	Life span (year)	Abundance	Modification	Purpose	Structure size	Decay time (year)	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	$5000 m^2$	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	$3000/m^2$	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)

(c): Ecosystem engineer collectives						
Taxon	Latin name	Body size (m)	Life span (year)	Modification	Abundance	Citation
Soils of mountains of Luquillo National Forest, Puerto Rico; Thickness = 1 m; Soil production rate = 0.1 m/1000 years; Decay time = 10,000 years						
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 et al. (2007)
Tabonuco	*Dacryodes excelsa*	30	75	Rock fracture, soil bioturbation	200/ha	Scatena and Lugo (1995)
Travertine dams and pools of Fossil Creek, Arizona; height = 3 m; growth rate = 0.01 m/year; Decay time = 300 years						
Cyanobacteria	*Synechococcus*	10^{-6}	0.3	Raise pH	$10^7/m^2$	Takashima and 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 and Pentecost (1999)

Abbreviations: ND, non-dimensional; Repro., reproduction.

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 behaviour 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, 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

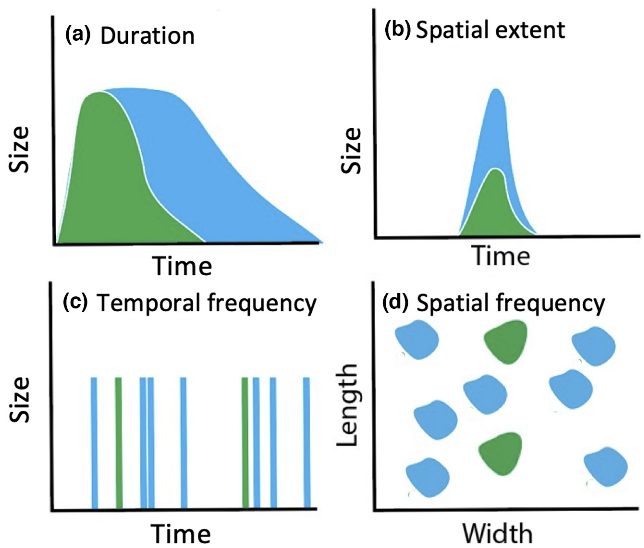

FIGURE 1 (a) Ecosystem engineering organisms can leave legacies that range from small (green) to large (blue) duration (a) and spatial extent (b), and from low (green) to high (blue) frequency through time (c) and through space (d). These three attributes—duration, spatial extent and frequency—of the modification contribute to the magnitude of the legacy.

(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 level 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). 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 Jr, 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 non-native 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 (2019) 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 & 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 life span 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 build-up 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 spatiotemporal 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-m 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 5000 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).

Behavioural traits can also affect legacies (Gribben et al., 2013). How conspecifics interact with one another is an important behavioural 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 catalyse 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 life spans 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/year), 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 behavioural 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 life span 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.

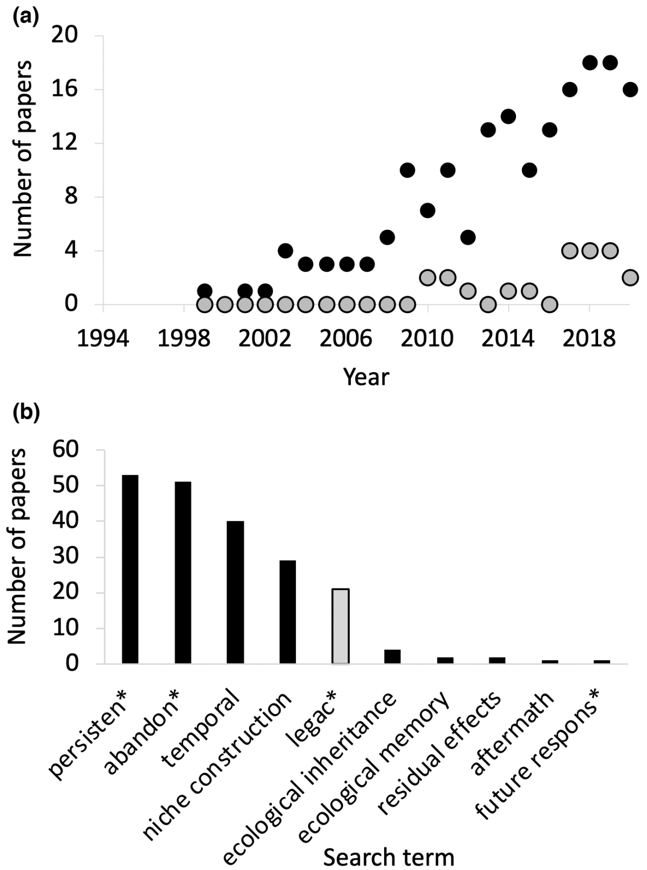

FIGURE 2 Summary of ecosystem engineering papers studying legacy effects from 1994 to 2020; see Appendix A for additional information. (a) The number of papers studying legacy effects through time. Black circles show all papers identified by any of the search terms in panel (a) and grey circles show 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.

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 such as '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, 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 | TOWARDS CONCEPTUALIZATION OF LEGACY IMPORTANCE

Although recent syntheses have begun to describe ecosystem engineering effects (Albertson & Allen, 2015, 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). Behavioural 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 life spans and body sizes. Below we explore a framework that links three key traits, living strategy, life span 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

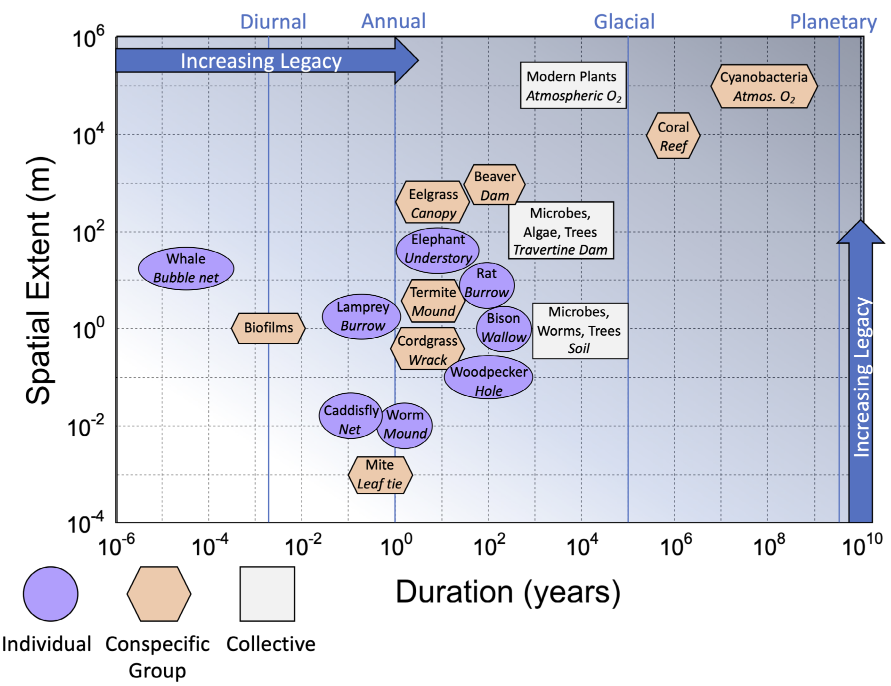

FIGURE 3 Duration of an engineered structure through time and its spatial extent determine legacy magnitude. Living strategies such as individuals (purple) or groups of organisms (orange) and collective actions of multiple organisms (grey), provide additional context for understanding ecosystem engineering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

producing organisms, the temporal magnitude of their legacy could be represented by the 5000 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 life span

Engineer life span 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 50 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, life span 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 life span, 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 analysed 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 life span 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

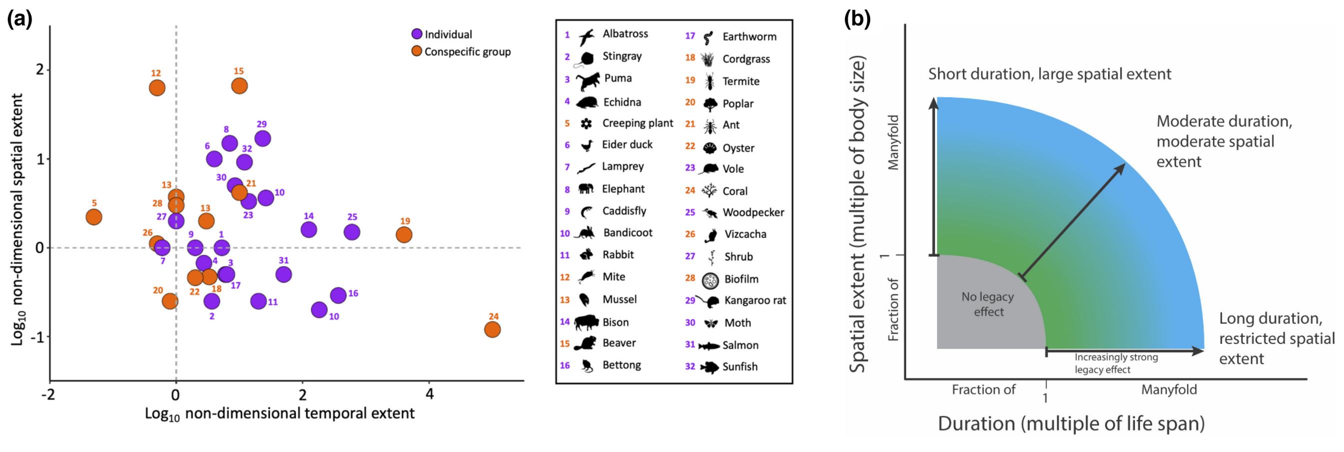

FIGURE 4 Non-dimensional framework for evaluating the strength of ecosystem engineering legacy effects. (a) Ecosystem engineering examples that illustrate the wide range of legacies documented in the literature, scaled by life span and body size of the engineer. Legacy effect is a function of structure 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 life span 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).

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 life span 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 3393 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; Wilkinson 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 life spans, 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 life span 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 life span 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. Modelling may provide a solution to some of these challenges.

4.3 | Feedbacks and modelling

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 behaviours will also be an important area of research moving forward (Franco & Fontanari, 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 molluscs 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).

AUTHOR CONTRIBUTIONS

Lindsey K. Albertson conceived the idea; All authors designed the research; Lindsey K. Albertson, Leonard S. Sklar, and Benjamin B. Tumolo collected the data; Lindsey K. Albertson led the writing of the manuscript; All authors contributed significantly to the writing, critically evaluated the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

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).

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SUPPORTING INFORMATION

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