Monitoring and modelling the effects of ecosystem engineers on ecosystem functioning

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Abstract

1. Ecosystem engineers modify biophysical environments, create novel habitats, and change biodiversity, with the ultimate effect of modulating critical ecosystem functions. This review describes and synthesises approaches, methodologies, and analytical frameworks for quantifying how ecosystem engineers drive ecosystem functioning.

2. We i) outline what variables to measure, how to measure them, and define the appropriate ecological and spatiotemporal scales for monitoring changes in both ecosystem engineers and ecosystem functioning; ii) illustrate experiments involving species exclusion or removal, addition or re-introduction, and comparative designs when experimental manipulation is not feasible; and iii) describe statistical, data-driven, and theory-driven approaches for estimating and forecasting the impact of ecosystem engineers on ecosystem functioning.

3. In the Anthropocene, humans are a salient example of an ecosystem engineer. We discuss how to leverage the ecosystem engineer knowledge in the context of current anthropogenic change for achieving conservation, restoration, and climate-mitigation goals.

4. We suggest evidence-based models and practises that can facilitate transformative changes in socio-ecological processes associated with ecosystem engineers. We conclude that implementing programs that monitor, forecast and apply the ecosystem engineer framework would sustain biological diversity and functional ecosystems.

1.   Introduction

Two and half billion years ago, the atmosphere consisted primarily of methane and carbon dioxide, without any free oxygen (Fischer, 2008). Then, cyanobacteria developed the capacity to perform photosynthesis, profoundly altering the course of life on Earth (Odling-Smee et al. 2003). Rising levels of atmospheric oxygen, a byproduct of photosynthesis, facilitated the development of aerobic respiration and the evolution of complex multicellular life (Soo et al., 2017). These remarkable events reveal a fundamental ecological principle: organisms are not passively subject to abiotic conditions, but rather they can also 'act' upon their surroundings, and change the environment. Organisms that are particularly successful at modifying their environment are often referred to as ecosystem engineers.

Formally, ecosystem engineers (EEs) are organisms that modulate the availability of resources to other organisms by causing physical state changes in biotic or abiotic conditions (Jones et al., 1994, 1997). In other words, EEs are organisms whose presence and activity significantly alter their biophysical surroundings or change the flow of materials and resources, thereby creating or modifying habitats and altering ecological processes (Coggan et al., 2018; Crain & Bertness 2006; Schöb et al., 2012; Wright & Jones, 2006). While all species modify their surroundings to some extent, EEs are more likely to have significant and long-term impacts relative to non-engineering organisms (Hastings et al., 2007). Yet, the broader impact of EE on biodiversity and ecosystem functions remains overlooked (Losapio et al., 2021a).

EEs can directly affect ecosystem processes through their own biophysical effects and indirectly shape the ecology and evolution of biodiversity across all levels of biological organisation (Odling-Smee et al. 2003; Desie2020; O'Brien et al. 2021). For example, leguminous plants (family Fabaceae) host mutualistic nitrogen-fixing bacteria in their roots, which enrich the soil and create 'islands of fertility' (Padilla & Pugnaire 2006). The presence of leguminous shrubs directly modifies nutrient levels in the soil, changes soil functioning, and alters microclimates via shading and water uptake, while also indirectly facilitating the recruitment of other plant species that ultimately attract insect pollinators and their predators (Lortie et al., 2016; Losapio et al., 2021b). In a different fashion, McCauley et al. (2012) documented a long chain of ecological interactions caused by ecosystem engineering on a remote atoll. There, native trees (the ecosystem engineer) attract roosting seabirds, which fertilise soil by depositing guano, resulting in coastal nutrient enrichment, increased

zooplankton abundance, and ultimately greater numbers of giant manta ray (*Manta birostris*). As in these examples and more broadly, diverse organisms acting as EE enhanced establishment, survival, and reproduction of other species, thereby supporting biodiversity across trophic levels and ecosystem services even across marine and terrestrial systems (Tab. 1). Thus, by nature of their definition, we postulate that EEs mediate complex interactions between the environment, biodiversity, and ecosystem functioning (Figure 1). Analogous to EE, the concepts of keystone species or foundation species reflect the importance of certain species in structuring ecosystems and driving their function (for more specific distinction, see Ellison, 2019). Despite the importance of EEs, ecological theory and experiments addressing ecosystem functioning often omit EEs' role in modulating resources and driving biodiversity (but see e.g., Bulleri et al., 2018; Kefi et al., 2008; Losapio et al., 2021a; Thomsen et al., 2018; Wright et al., 2006).

Ecosystem functioning (EF), also referred to as ecosystem functions, represents the interactions between biotic and abiotic components of an ecosystem by addressing structures and processes of living organisms as complex social–ecological systems (de Groot et al., 2002; Millenium Ecosystem Assessment, 2005). EF includes many processes such as biomass production, trophic transfer through plants and animals, nutrient cycling, water dynamics and heat transfer (IPBES, 2019). This concept is used here in the broad sense and it can thus be taken as being synonymous with ecosystem properties or ecosystem structure and function. Researchers often consider two aspects of EF: internal functioning of ecosystems (referring to matter cycling, energy transformation and information flows arising from the combined activity of living organisms), and extrinsic functioning of ecosystems (referring to ecological components, properties and processes providing benefits to humans). Most of the time, the internal and extrinsic functions overlap, and EEs affect both. For instance, air regulation functions of forests maintain both human and ecosystem health. Here, we overcome this internal versus extrinsic dichotomy, considering the multiple benefits EEs (and associated biodiversity) provide to social–ecological systems, that is for both people and the planet (IPBES, 2019).

There is consensus that increasing biodiversity contributes to increasing both functional and healthy ecosystems together with increasing economic revenue and human health (Binder et al., 2018; Huang et al., 2018; Kilpatrick et al., 2017; Tilman et al., 2014). In the context of biodiversity–ecosystem functioning relationship (BEF) research, EF originally

referred to net primary productivity or more often above-ground biomass production (Hooper et al., 2005). However, despite the abundance of research investigating the BEF relationship (see e.g., Brandl et al., 2019; Huang et al., 2018; Wagg et al., 2019; Tilman et al., 2014), EEs are often viewed as exceptional case studies, rather than key drivers supporting ecosystems structures and their functioning.
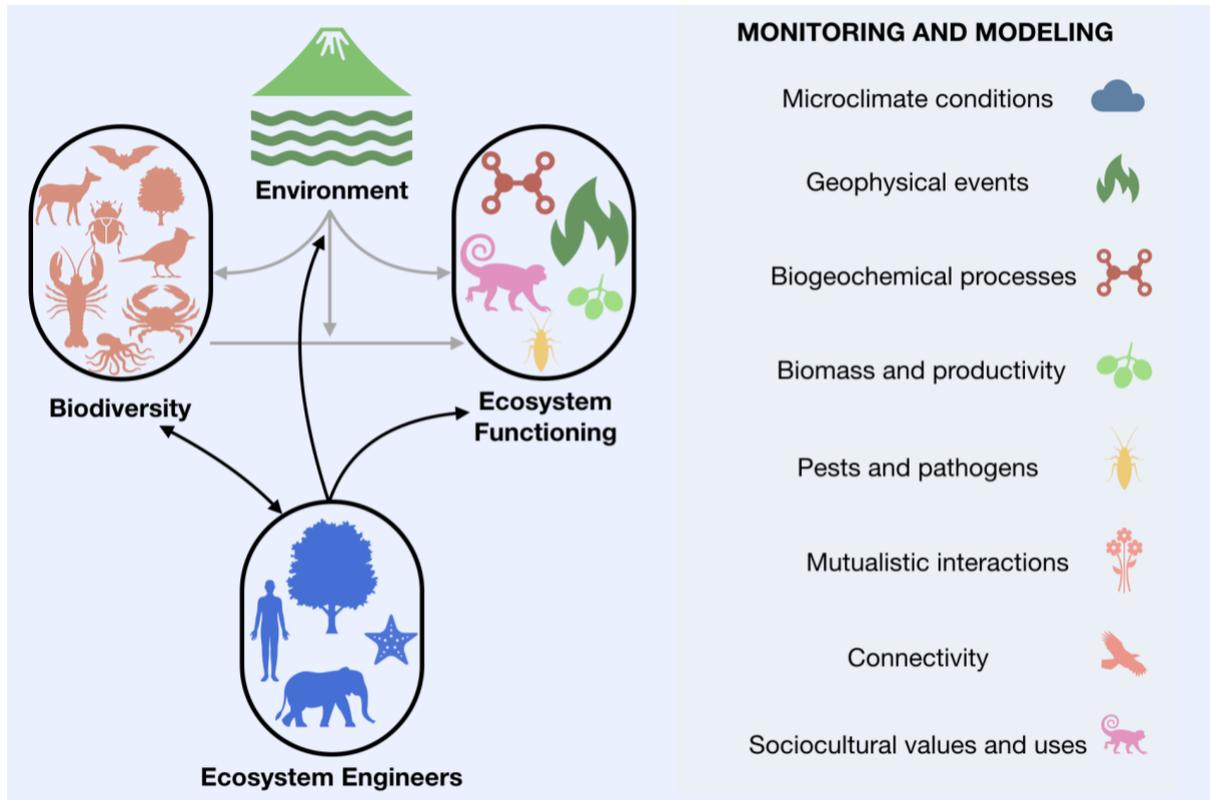

Figure 1. Left: Ecosystem engineers mediate complex relationships and feedback among the 'abiotic environment', biodiversity, and ecosystem functioning. Black arrows represent interactions considered in this paper, promoted by ecosystem engineers. Grey arrows represent relationships mediated by the abiotic environment, which are outside the scope of this paper. Right: Ecosystem engineers support diverse ecosystem functions (colored symbols), sorted in non-exclusive types of variables to be monitored and modelled.

In the context of BEF studies, the contribution of each species to EF is measured as species performance along a single niche axis (Loreau & Hector, 2001; Schmid et al., 2002). Analogously, the contribution of EE to EF can be measured similarly to BEF approaches by using other measures of species performance that affect functioning (Losapio et al., 2021a). For instance, flower visitation rate or arbuscular mycorrhiza fungi colonisation are measures of ecological processes that have been shown to contribute to greater EF (Losapio et al.,

2021b; Padilla & Pugnaire 2006). Following the knowledge of BEF relationships (Hooper et al., 2005; IPBES, 2019) as well as the contribution of EE to both biodiversity and EF (Fig. 1), it is reasonable to argue that supporting EEs is mutually beneficial to both environmental health and human well being. Likewise, humans themselves act as EEs, and ecosystem engineering by humans can increase or decrease EF (Ellis, 2015). Therefore, including the role of human activities from an EE perspective could aid conservation to mitigate environmental change and restore ecosystems and their supporting ecological processes.

Here, we synthesise approaches, methodologies, and analytical frameworks for quantifying how EEs drive EF. Moreover, we discuss how to measure and monitor anthropogenic effects on EEs and their EF in the context of global environmental change. Our goal is to present an integrative view of EEs and provide a road map for mainstreaming the inclusion of EE in EF studies.

2. Monitoring ecosystem engineers and ecosystem functioning

In order to study the ecological effects of EEs, it is necessary to monitor simultaneous changes in both EEs and EF. Due to the inherent complexity of EF, establishing a clear relationship between EEs and their associated impact on EF requires the careful design of monitoring frameworks. These frameworks may include experimental, comparative, or modelling studies, as detailed in sections 3 and 4. The main components of monitoring programs must address what to measure, where, and how (Walter & Scholes, 2017). These are informed first and foremost by the study goals, which will determine which response variables to measure. Next, it is important to consider the biological and spatiotemporal scales at which the response should be measured. Lastly, researchers must consider ecological context and additional covariates which may modulate the effects of EEs on EF.

a.   Study goal and which variables to measure

Study goal refers to the purpose or desired outcome of the monitoring efforts. When examining the relationship between EEs and EFs, study goals may include, among others: fundamental research addressing novel hypotheses, long-term survey programs for conservationists and managers, applied research in conservation biology, or the development and implementation of strategies for addressing socio-environmental issues (Lindenmayer et al. 2013). In any case, monitoring efforts must establish how changes in EF

variable(s) depend on and are caused by changes in EEs. Furthermore, both EE explanatory and EF response variables must be clearly defined, reliably measurable, and quantifiable.

Researchers may be directly interested in EEs themselves, or they may be interested in specific EFs in which EEs may play a role. If the study does not already entail specific target EEs or EFs of interest, first we need to ask: which species may act as EEs? And, which EFs may they affect? Then, we need to consider the direction and magnitude of that effect: is the EE causing increases or decreases in EF, and by how much? Furthermore, are those effects increasing or decreasing over time, and at what rates? Are those effects homogeneous or heterogeneous across space? Finally, to understand the mechanisms of EE–EF interactions, what are the specific causes of the EE effects we are observing?

In order to answer these questions, we must select the appropriate variables to measure. Since we are interested in the effect of EEs on EF, we must measure properties and changes associated with EE that lead to modification of the EF state. These include one or more explanatory variables representing EE impact and one or more response variables representing the EFs of interest. EE and EF metrics can be categorised based on the scale of biological organisation at which variables are measured.

In plant-engineered habitats, such as kelp forest, seagrass prairie, mangrove forest, or woodland, the presence and activity of plants affect physical structure, and ultimately shape the functioning of ecosystems (Jones et al., 1997). Yet, it is important to monitor and measure not only EE presence/absence, population size, and density, but also other structural and functional attributes that determine the engineering impact of plants and fungi on EF (Walter & Scholes, 2017). This includes, as for animal EEs, the quality and quantity of (non-necessarily trophic) resources that are directly or indirectly controlled, the underlying mechanisms, as well as the abundance and richness of other species and communities depending on them (Jones et al., 1997). The increased EF should be measurable as and related to a change in plants and associated state variables.

Hence, key plant variables may include: (i) at the population/species level, population size (i.e., individual abundance) together with germination, growth, survival, fecundity, and age; sexual reproduction parameters including flower/inflorescence number and size, pollen and nectar production, flower visitation rate, fruit and seed set (i.e., number, weight, and viability of seeds/fruits), and fruit dispersal; root depth and root colonisation; (ii) at the community level, community composition (i.e., species presence and

their abundance), diversity, cover, height, standing biomass, and yield; rhizosphere microorganism composition; plant defences (spines, trichomes, secondary metabolites), herbivory (leaf damage and consumption, galling, mining), and pathogen prevalence and load (e.g., mildew, leaf spot, necrosis); (iii) at the landscape scale, land-use type and cover, remotely-sensed data such as NDVI, EVI, GSL, disturbance and degradation. Plants can engineer not only while alive, but also while dead and/or decaying. For example, plants and plant parts (e.g., litter, bark, downed logs) substantially increase biodiversity and influence biogeochemical cycles via, for instance, providing organic matter to saproxylic fungi, bacteria and insects.

When addressing animals acting as EE, we need to monitor and measure changes in population-, community-, and landscape-scale metrics (Figure 2). The most relevant factors for EE–EF studies are usually natural history, activity, body size, demography, spatial distribution, and residence time (Jones et al., 1994; Moore et al., 2006; Hastings et al., 2007). Key design features of EE natural history important to be monitored are the degree of mobility and sociality, the formation of colonies and the decay rate of patches (Tarnita et al., 2017; Li et al., 2021). Other natural history aspects of EE biology include consumption, ingestion, and production rates associated with their holobiome and ecological guild (e.g., herbivore, secondary consumer, top predator, scavenger, pollinator or seed-disperser, symbiotic partners). Depending on the EE species-specific activity (for an overview, see Jones et al., 1994), characteristics of animal EE behaviour to be monitored include type and frequency of their activity such as burrowing, tunnelling and mixing (Moore et al., 2006; Li et al., 2021). Activity monitoring includes recording the kind of structures formed (e.g., woodpecker holes, cavity nests), the formation rate of structures (number of constructs over time, size distribution), and the durability of constructs in the absence of EE (Larsen et al., 2021). For instance, this process includes monitoring the size and number of dams built by beavers, the growth of and distance between 'cathedral mounds' built by termites *Nasutitermes triodiae*, the volume and movement of soil particles and sediments by earthworms, the density and frequency of nests digged by salmons, amount and properties of faecal pellet, scat and guano deposition by seabirds, frequency and intensity of trampling and pawing by elephants. Further metrics to be monitored include individual physiological conditions, functional diversity, resource use, change in distribution and range shift (Tab. 1).

Intraspecific variation in body size modulates the impact of EE on EF (Cozzoli et al., 2018). Although small animals can have big impacts, and viceversa big animals may have negligible impacts, monitoring EE body size can also inform multiple biological rates such as growth, reproduction and mortality (Bulleri et al., 2018). Likewise, population biomass needs to be tracked as it can predict fundamental EF such as disease regulation and the structure of animal–plant mutualistic interactions (Dirzo et al., 2014; Genes et al., unpublished data). As for the case of seabirds acting as EE (e.g., little auk *Alle alle*) via guano-derived nutrient input (González-Bergonzoni et al., 2017), it is also important to consider changes in temporal and spatial feeding and migratory patterns (e.g., nearshore or pelagic, seasonal dynamics). In fact, the spatiotemporal distribution of nutrients across terrestrial and aquatic ecosystems during bird flights is affected by environmental change (González-Bergonzoni et al., 2017).
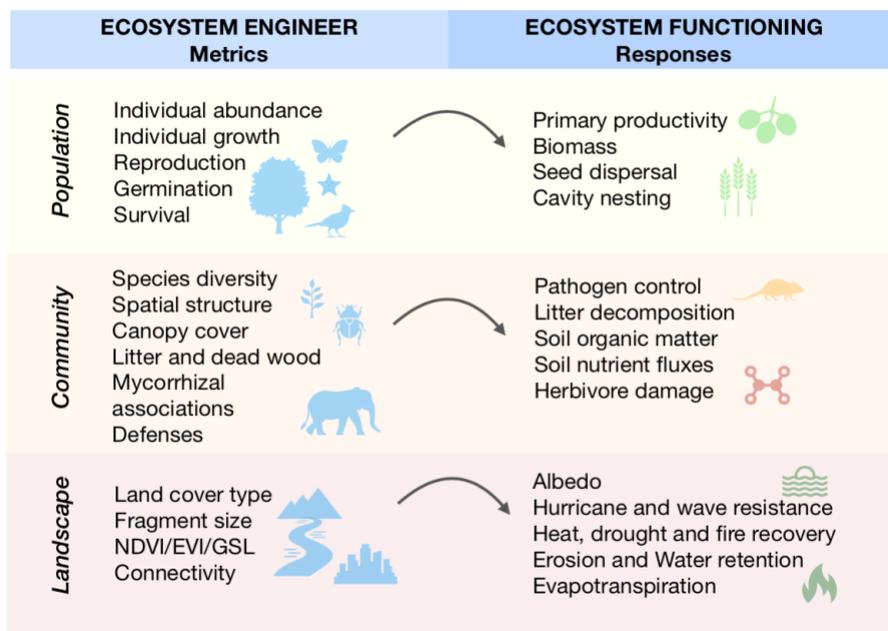

Figure 2. Example population-, community-, and landscape-scale metrics of ecosystem engineers and associated ecosystem functions.

Functions of interest broadly include: (i) regulation of biogeochemical processes (e.g., oxygen, water, and carbon cycling), physical climate systems (e.g., temperature, humidity, radiation), and ecological processes (e.g., pollination, seed dispersal, biological control); (ii) creating and providing habitats (e.g., nursery and refugium); (iii) production (e.g., food, renewable resources, drugs), and (iv) cultural, non-material development and

enrichment (e.g., recreation, aesthetic and artistic inspiration, scientific research and education). Associated to the diversity of functions ecosystems provide (de Groot et al., 2002; IPBES, 2019), EF variables usually measured include (Fig. 2, Tab. 1): biomass production, primary and secondary productivity, carbon stock, nutrient fluxes, water retention, UV reflection, air and water pollutant detoxification, soil erosion, sedimentation, pollination, seed dispersal and predation, herbivory, pest prevalence and incidence, cavity nesting, use for scientific, educational, historic, spiritual, and recreational purposes.

A single EE species can provide multiple functions at the same time, as illustrated by the case of mangrove forests (Fig. 3). Mangroves are tropical intertidal forested wetlands which play a key role in nutrient cycling, carbon storage, habitat provisioning, and shoreline protection. For example, mangroves shape coastal geomorphology through the production of organic matter and the retention of mineral sediment, thereby supporting soil accumulation and adaptation to sea level rise (Kraus et al. 2013). Due to their deep organic soils, mangroves are among the most carbon rich ecosystems on Earth, containing a mean of ~850 Mg C ha-1 (Kauffman et al. 2020). By occurring at the interface of terrestrial, marine, and freshwater ecosystems, mangroves support substantial biodiversity and cross-ecosystem linkages. For example, mangroves serve as important nurseries for commercially important marine fishes (Laegdsgaard and Johnson 1995) and support large numbers of colonial nesting waterbirds which vector nutrients between land and sea (McFadden et al. 2016).

All these effects can be calculated on a per capita (individual), per population (species), or per space unit (community and landscape; e.g., m2, km2) basis depending on the goal and scale of the monitoring framework. For an extensive overview on how to specifically measure plants, animals, and soil microorganisms, see Pérez-Harguindeguy et al. (2013), Halbritter et al. (2020), and Walters & Scholes (2017). Next we will discuss how scale (both biological and spatiotemporal) and context can help inform which explanatory and response variables to measure and how they are sampled.

b. Biological and spatiotemporal scales

Fundamentally, we seek to quantify how much change is occurring in both EE and EF, and then to understand how, where, and when that change occurs. A monitoring framework for assessing these effects should be a repeatable scheme, which can be based on existing

ecological (Lindenmayer & Likens, 2010; Lindenmayer et al., 2013), ecosystem (Eyre et al. 2011; Sparrow et al. 2020), and biodiversity (Pereira et al. 2013; Walters & Scholes 2017) monitoring frameworks.

Scale may strongly influence the selection of relevant explanatory (EE) and response (EF) variables (Gonzalez et al., 2020). In order to determine causality between EEs and EF, it is necessary to establish the scope (both spatio-temporally and biologically) upon which the relationship takes place. First, consider potential explanatory variables, in this case a quantifiable change in some EE. An important step is to determine the biological scale upon which potential EEs mediate or modify an EF of interest. For example, if a single species directly participates in the provisioning of an EF, the biological scale is narrow. In these cases, it may be appropriate to incorporate explanatory variables which quantify measures of individuals (e.g. body condition, survival, reproductive output)(Fløjgaard et al. 2017). In studies where the focal EF is mediated by a multitude of species interactions occurring simultaneously, the biological scale is much broader. Here, explanatory variables which consider community-level metrics such as species richness and composition are often employed.

While biological scale is key for determining suitable explanatory variables, spatio-temporal scale is often important for selecting reasonable response variables. Once measures of an EE are selected as potential modifiers of an EF, the main focus then becomes being able to detect those changes (i.e. selecting a scale upon which the response is observable). This can depend on the species identity of the EE and on the explanatory variables chosen. Biogeography, distribution, behaviour, and phenology of EEs can all influence the spatio-temporal scale upon which changes in an EF are observable. For example, the scale of observability for the effects of elephants on nutrient redistribution is much different than the one for the effects that dung beetles have on the same process. In addition, the identity of the focal EF itself can also determine this scale of observability. Non-linear relationships between EE and EF as well as dissimilar effects of co-existence, connectivity, and temporal autocorrelation can all impact the scale at which potential responses are detectable (Gonzalez et al., 2020). Ultimately, determining reasonable scales and selecting appropriate explanatory and response variables is highly dependent on an understanding of context and study systems. Accounting for this context dependency is the next step in effectively monitoring the relationship between EE and EF.
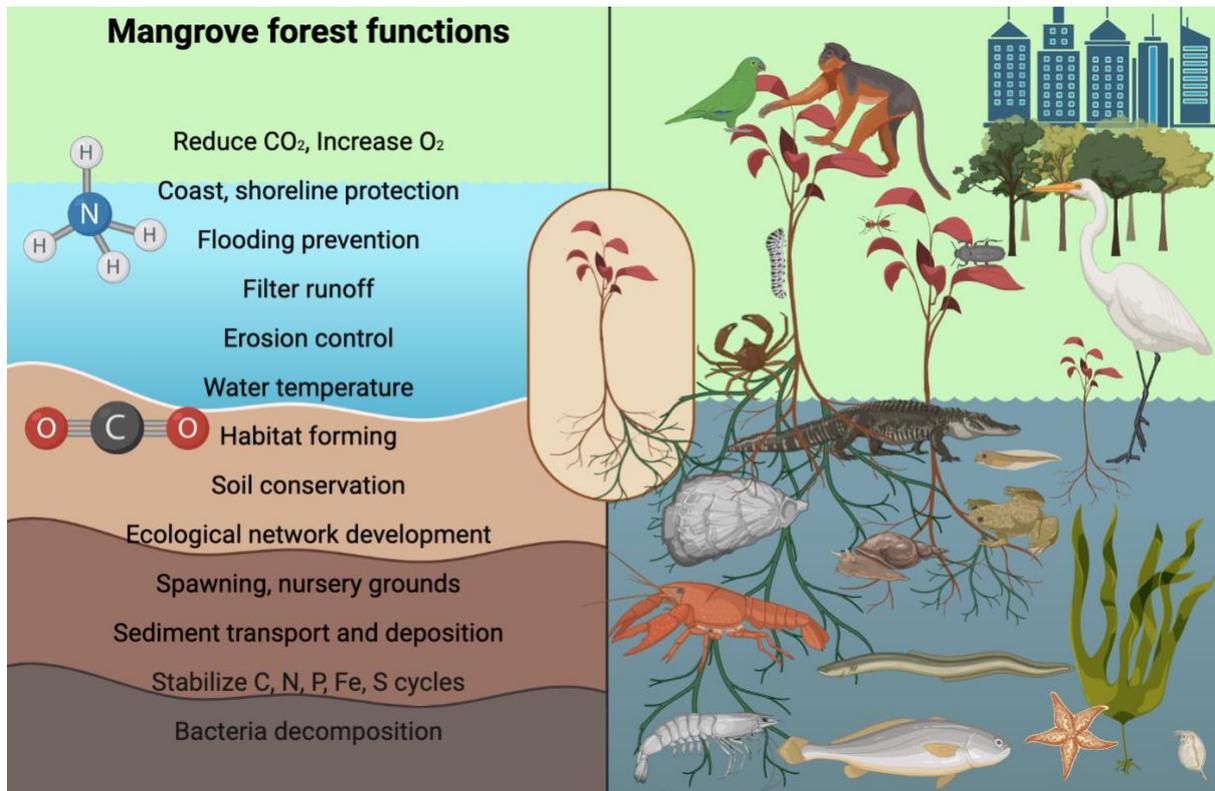
Figure 3. Impact summary of mangrove, a classic ecosystem engineer, on ecosystem functioning.

c. Match context

EEs may have variable effects on EF depending on the environmental context in which the interaction takes place. For example, the engineering impacts of the invasive Pacific oyster (*Crassostrea gigas*) can be both positive and negative, and the direction and magnitude of these impacts are dependent on the invaded system's substrate type, abiotic stressors, and presence of other EE species (see Padilla, 2010 for review). Environmental context must therefore be considered when selecting suitable response variables. Determining and accounting for the environmental context may require information about species natural history, biophysical conditions, biogeochemical processes, social dynamics, and a multitude of other environmental factors. Considering this context is crucially important because of its influence on both EEs and EF, as well as the relationship between them. When designing monitoring frameworks, environmental context is key for evaluating program scope, variable relevance, and overall feasibility (Lindenmayer et al., 2013).

It is also important to consider the socio-ecological context in which EEs exist. For example, North American beavers (*Castor canadensis*) are EEs in their native range, yet are

considered damaging invasives in their exotic range in southern South America. Despite these differing perceptions, beavers in North and South America engineer similarly and have similar effects on biodiversity and EF (Larsen et al., 2021). In both areas, sites with beaver have greater soil organic matter, reduced canopy cover, and greater herbaceous plant and macroinvertebrate richness. However, beavers are perceived differently by stakeholders in South America, where beaver-altered ecosystems are less socially desirable than uninvaded forest ecosystems (Anderson et al. 2009). Conservation is a value-driven process, and so an EE can have positive effects on EF, yet still have undesirable socio-ecological impacts.

Table 1. Summary of ecosystem engineer species (EE) and related ecosystem functions (EF) that are often measured and their scale.

EE	EF	Measures	Scale	References
Ants	Nutrient cycling, plant recruitment	Seed and carrion removal ~ ant abundance	Community, Landscape	Griffiths et al. 2017
Beaver	Hydrological and riparian structure	Aquatic habitat connectivity ~ active beaver ponds	Community, Landscape	Larsen et al., 2021
Corals	Wave energy dissipation	Wave size ~ Reef Structure Type & Reef Location	Community	Ferrario et al., 2014
Cordgrass	Biodiversity	Invert Diversity ~ presence/absence of cordgrass + native vs invasive	Community	Brusati and Grosholz 2006
Cushion plants	Pollination	Pollinator diversity ~ presence/absence cushion plants	Community	Losapio et al. 2021a

Dung beetles	Nutrient cycling	Plant growth ~ Dung beetle abundance * dung beetle size	Community	Nichols et al. 2008; Johnson et al. 2016
Earthworms	Nutrient cycling	Litter properties ~ Earthworm biomass/density	Community	Desie et al. 2020
Elephants	Ecosystem structure	Forest structure (canopy cover, stem density) ~ Elephant biomass	Landscape	Daskin et al. 2016
Kangaroo rat	Biodiversity	Plant and consumer diversity ~ rat density + burrow density	Community	Prugh and Brashares 2012
Kelp forest	Biodiversity	Species richness ~ Kelp biomass over time	Population, Community	Miller et al., 2018
Mangroves	Carbon storage	Total C ~ Tree biomass + Soil depth + precipitation	Community, Landscape	Kauffman et al., 2020
Pacific Salmon	Nutrient cycling	Nutrient transfer from sea to land ~ salmon run size + consumption rate by terrestrial consumers * consumer identity	Community, Landscape	Walsh et al. 2020; Cederholm et al. 1999

Retama broom	Pollination	Visitation rate ~ Retama presence + plant diversity	Community	Losapio et al. 2021 b
Seabirds	Nutrient cycling	Plant nutrient levels ~ Bird biomass	Landscape	Young et al. 2010
	Primary production	Primary production ~ Bird colony presence	Population	González-Bergonzoni et al. 2017
Seagrass meadows	Sediment accretion	Sediment ~ Presence + Density	Population, community	Bos et al., 2007
Termite	Vegetation growth	Plant density ~ fairy circle distance	Community, Landscape	Tarnita et al. 2017
Vultures	Nutrient cycling, disease regulation	Carcass removal rates ~ vulture abundance * species identity	Community, Landscape	DeVault et al. 2003; Houston and Cooper 1975

3. Experimenting

We can experimentally test how EEs influence EFs by changing EEs and measuring the resulting impacts on EF. Although inferring causal relationships and quantifying effects do not always and necessarily require altering the study subject, experimental manipulation is central to inductive reasoning (Bolker, 2008). Experiments are the most rigorous way of identifying the mechanisms underlying the role of EE in driving EF. This way, EEs are considered as the treatment (i.e., independent variable) under scrutiny responsible for inducing changes in EF, here the outcome of interest (i.e., dependent variable).

We identified three broad possible experimental-manipulation types: (i) exclusion or removal, (ii) addition or reintroduction, and (iii) comparative, semi-experimental designs for

when experimental manipulation is not feasible. In all these cases, the usual approach is to manipulate the presence, abundance, density, identity, or richness of EE.

a. Exclusion or removal experiments

Excluding or removing EEs is an experimental approach to quantify how much and how EF depends on EE. Exclusion methods are usually adopted for mobile EEs (animals) while removal methods are used for sessile ones (plants and microorganisms). However, the idea behind exclusions and removals is the same: making a treatment where EE is absent. The experiment should also include the natural conditions in which EE is not manipulated, which will serve as a positive control (Losapio et al., 2021a). This set-up also reveals what would happen to EF in case of EE loss or extinction.

Fences that exclude large mammal EEs from the ecosystem provide opportunities to examine the relationships between wildlife loss (i.e., defaunation) and different EFs, including productivity, fire suppression, and disease regulation. For instance, elephants (*Loxodonta africana*) engineer the African savanna and woodland by physical ground disturbance and toppling trees. The absence of elephants ultimately changes seedling recruitment, seed dispersal, community dynamics, nutrient cycles, and fire regimes (Jones et al. 1994; Cloverdale et al. 2016). An outstanding long-term exclusion study example is provided by the Mpala Research Centre in Kenya, where Young et al. (2014) observed that experimental defaunation increases the risk for zoonotic diseases that are spread between animals and humans. Rodent population doubled in the absence of large mammals and thus the number of infected fleas with *Bartonella* bacteria carried by rodents had also doubled (Young et al., 2014). This experiment highlights that the loss of large mammalian EEs ultimately increases the risk of human disease (Dirzo et al., 2014).

Excluding smaller EEs like soil and marine macrofauna can also be achieved. Manipulation usually takes place at fine spatial scales (order of squared metres) and makes use of fine meshes. For example, crabs are EEs that positively affect soil redox potential and soil oxygen availability via their burrowing activity (Daleo et al. 2007). The exclusion of crabs (*Chasmagnathus granulatus*) reduced plant growth and the colonisation of plant roots (*Spartinia densiflora*) by arbuscular mycorrhizal fungi, indicating that crabs mediate species interactions and in doing so modulate ecosystem productivity.

b. Addition experiments

We can experimentally test how EEs influence EF by manipulating their presence or abundance and measuring the resulting impacts on EF variable(s). Translocating EE species to study sites where they were previously absent is an effective way of examining their impact on abiotic and biotic processes, as found in studies using seaweeds and seagrasses (Bos et al. 2007, Layton et al. 2019, Shelamoff et al., 2019). Addition experiments also consist of translocating different treatments of marine kelps that varied in area size and kelp density and measuring abiotic conditions under each treatment, and kelp growth and survival. Layton et al. (2019) found that larger patches of a marine kelp, and to a lesser extent, larger kelp density, reduced water flow, sedimentation, and irradiance, which positively impacted growth and survivorship of juvenile conspecifics, highlighting a case of EE intraspecific facilitation. Similarly, transplanting canopy-forming kelp (*Ecklonia radiata*) in artificial reefs demonstrated how this EE increases diversity of other plant and animal species (Shelamoff et al., 2019). By reducing benthic light and suppressing competition from turfing algae, kelp EE particularly facilitates critical and crucial species as reef-forming oysters (*Ostrea angasi*).

The ongoing spread of exotic species provides opportunities for conducting additive experiments. In this context, studies of exotic EEs may provide important guidance for invasive species management, as well as generate basic knowledge regarding the effects of EEs on EF. Studies addressing invasive EEs are increasingly common, though terrestrial and marine ecosystems are more frequently studied than freshwater ecosystems (Emery-Butcher et al. 2020). Despite exotic species having well-known negative impacts on biodiversity and ecosystem function, the effects of exotic EEs are variable and strongly context-dependent. For example, in some contexts, invasive EE species can have some beneficial effects. In North American deserts, invasive feral equids were found to dig wells as deep as 2 m to access groundwater, increasing water availability to other animals, and becoming riparian tree nurseries (Lundgren et al., 2021). Although not native, these equids provide EF that support biodiversity, and may be able to replace function that was lost with large vertebrate extinctions.

Similarly, researchers can take advantage of ongoing EE species reintroductions, which work as additive experiments, specially when study design allows comparison of before and after reintroduction, or to similar sites where EE species is extirpated. These

experiments can be useful both to elucidating the role of EE, but can also inform ecosystem restoration and associated policies and practises.

c.   Comparative design

Comparative designs (e.g. time series or 'space-for-time' studies) that utilise data across temporal or spatial replicates can be employed to examine the influence of EEs on EF when the addition or removal of an EE has already occurred, as in the case of species invasions or exploitation, or if the addition or removal is logistically or environmentally infeasible, as in the case with protected species and areas. For instance, Brusati and Grosholz (2006) investigated how native and invasive hybrid cordgrass (*Spartina*) influenced abiotic factors and infauna invertebrate densities by comparing uninvaded and invaded sites. The study found that while both species acted as ecosystem engineers, native cordgrass promoted while invaded cordgrass reduced invertebrate diversity, highlighting results that would otherwise be difficult to pursue and justify with manipulative experiments that would require the movement of an invasive species. Exploitation of a focal species can also opportunistically provide key insights about their role as an ecosystem engineer. Estes and Palmisano (1974) compared sites where sea otters were previously overexploited, but had rebounded, to sites where otters remained rare and found that otters facilitated macroalgae abundance indirectly by regulating herbivorous urchin populations.

Considering that EEs are more likely to have more persistent effects on EF than non-engineering species (Hastings et al. 2007), time series studies are particularly relevant. For instance, Miller et al. (2018) used a 15 year time series of kelp forest community data and employed structural equation modelling to demonstrate that kelp biomass is positively associated with species richness, and that kelp mediates this relationship by shading out understory algae that would otherwise compete with sessile invertebrates. This combination of comparative designs with modelling provides stronger mechanistic inference, as we discuss further in the coming section.

4. Modelling

Modelling the effects of EEs on EF serves the purpose of both determining scientific explanations for observed relationships and enabling predictions. This requires integrating aspects of both causal (i.e., explain cause and effect relationships) and mechanistic perspectives (i.e., identify the drivers of the relationship).

a. Causal relationships

Identifying causal relationships is a necessary step to formulating mechanistic explanations of ecological processes. The first aim is to establish dependency relationships between two variables, without consideration of the mechanism involved in the connection between the cause and its effect. This means addressing first what would happen to EF if EE is modified or remains stable.

To assess whether specific changes in EEs influence EF, we can use the general form of $Y = F(X)$, where ecosystem functioning Y responds to ecosystem engineers X. A simple model to parametrize this relationship is a univariate linear regression, such as $Y = \alpha + \beta X + \varepsilon$, with $\varepsilon \sim N(0, \sigma^2)$. Here, α is the intercept for the mean value of an EF response (dependent) variable Y in the absence of ecosystem engineers, β is the magnitude (i.e., slope) of the effect of EE explanatory (independent) variable X on ecosystem functioning. The term ε is the associated error (i.e., compound error, including measurement accuracy and precision and unaccounted population variability associated with third factors), which is assumed to be normally distributed with mean 0 and variance σ^2. Parametrizing this model (i.e., inferring estimates of α and β with confidence intervals) will tell us how much an EF variable is changing for each unit change in EE. The parameters of this linear regression can be estimated using a least squares approach, by a maximum likelihood estimation procedure, or MCMC methods (Zuur et al., 2009). In all cases, the parametrized model is then tested for significance using a χ^2 test of model fit (for an in-depth discussion, see Bolker, 2008; Gotelli & Elisson, 2012; Zuur et al., 2009).

Although such a simple univariate model can provide a basis for prediction, it fails to provide all the information that is potentially relevant to a fundamental understanding of the relationship between EE and EF. Our aim is to identify the degree to which invariant relations change under certain –and potentially, all foreseeable– circumstances. Those circumstances being the climatic, biogeographical and historical background, the

environmental context, the presence, extinction or invasion of other species, random variation among individuals and populations, properties of EF and attributes of EE studied, and also the specific interactions between any of those factors. This information can be formalised as $Y = F(X_i)$, where X_i is the set of multiple, independent variables *i* relevant to understanding and predicting the effects of EE on the EF dependent variable *Y*. For instance (Hooper et al., 2005), productivity (*Y*) is influenced by EE density (X_1) and varies with altitude (X_2), which can explain part of the variation observed in productivity regardless of EE density. Such additive model would be in the form of $Y = \alpha + \beta_1 X_1 + \beta_2 X_2 + \varepsilon$, where β_1 and β_2 indicate the strength of the relationships between EF and EE and EF and altitude, respective. Furthermore, the effects of EEs on productivity changes with altitude too (Hooper et al., 2005). That is, the EE–EF relationship changes with or depends on altitude. The model now needs to account for both the additive effects of altitude and the dependency of EE effects on altitude. By including the statistical interaction, the model is formulated as $Y = \alpha + \beta_1 X_1 \times \beta_2 X_2 + \varepsilon$, where $\times$ denotes the interaction term $\beta_1 \cdot \beta_2$ between EE density and altitude.

Yet, EE density and other environmental and biotic variables are most likely measured at different resolutions, and hence cannot be treated on the same level as they may have effects on different scales. In addition to those limitations, simple regression models cannot handle complex study designs and monitoring schemes (Zuur et al., 2009). For instance, it is often necessary to monitor and measure the same EE populations and communities over time (e.g., time series data such as tree recruitment or fish catch) or resample the same EE individuals (e.g., mark and recapture, tree growth). Furthermore, biological replicates may be spatially correlated (e.g., certain individuals may be physically closer or further away from each other) or may have observations that are not independent (e.g., EF measured before and after the experimental manipulation/treatment). Statistical replicates may be heterogeneous (e.g., high variation within EE populations or different EE genotypes), paired or grouped (e.g., EF measured with matched-pairs or block designs, respectively), or subsets of larger populations (e.g., certain EEs or combinations of EEs are chosen from a larger pool). Finally, EF response variables can have a different distribution than a normal one, such as in the case of count data (abundance, richness) or presence/absence data (occurrence, survival, mortality) which are better represented by Poisson, Negative

Binomial, Gamma, or Binomial distributions. All these factors lead to violation of model assumptions because linear regression models cannot handle error terms ε that are heterogeneous, not normally distributed, nor hierarchical data with observations that are not independent (Bolker, 2008).

Thus, linear regression must be replaced with mixed modelling. Generalised mixed models (i.e., hierarchical linear models or multilevel models) better support analysis of a dependent variable in cases of repeated measurements, random effects , hierarchical effects, heterogeneous variance, or spatial correlation (Zuur et al., 2009). These mixed models consist of a fixed term and a random term, such that $Y = F(X, Z)$, where the EF response variable Y is a function of the fixed term X and a random term Z. The fixed term is identical to a linear regression, with the predictor variables X as described above, while the random term Z contains components that allow to model variance heterogeneity, nested data, temporal correlation, spatial correlation, and random noise.

To account for heterogeneity of variance (i.e., non-normally distributed residuals), thus allowing different residual variation, the random term needs to incorporate a specific variance component structure. For instance, the variation in model residuals may increase (or decrease) with increasing altitude such that $\varepsilon \sim N(0, \sigma^2 \times X_2)$, or change across different j altitudinal belts such that $\varepsilon \sim N(0, \times \sigma^2_j)$.

Research and monitoring programs often involve large, complex and multiscale designs spanning different communities, sites, and regions (see e.g., Walter and Scholes, 2017). EF studies often involve many blocks of plots or transects for each habitat within each biome. Measurements taken according to such hierarchical, multilevel structure (plots within blocks with habitat within biome) lead to nested data (Zuur et al., 2009). This way, EE identity or functional group vary among biomes, among habitats, and among habitats within each biome as well as EF changes among blocks within each habitat and biome. Furthermore, the effects of EE on EF may vary within biomes and across habitats. Therefore, we need to specify in the random term that each habitat and biome can have a different EF–EE slope b and allow for a random shift around the intercept a across habitats within biomes. It follows that $y_{ijk} = \alpha + a_k + a_{j|k} + (\beta_1 + b_k + b_{j|k}) X_1 + \varepsilon_{ijk} + \varepsilon_k + \varepsilon_{j|k}$ where y_{ijk} is the EF value measured at ith plot for each habitat j within each biome k.

Furthermore, such a type of nested design together with time-series and other ecological frameworks involving multiple locations measured several times leads to spatially

and temporally correlated data. Indeed, EEs and associated EF values that are closer to each other (e.g., EEs living within the same habitat or EF measured within the same season) are more likely to be more similar to each other than EEs and EF that are measured further apart. Thus, we need to include a temporal or spatial residual correlation structure to the model allowing residuals from different time or space point to covary (Zuur, 2009). This is accomplished by modelling $cor(\varepsilon)$, a correlation matrix for residuals that includes a specific correlation function. There are different types of parameterization for the correlation function and resulting residual correlation matrices (Zuur, 2009), and their use depends on the type of data and the ecological phenomenon. For time correlation, the most common one is the auto-regressive model of order 1, which models the residual at time s as a function of the residual of time $s - 1$ along with random noise. For spatial correlation, an usual option is an exponential correlation function in which the variance between two observations scales exponentially with the euclidean distance between them (for full description, see Zuur, 2009).
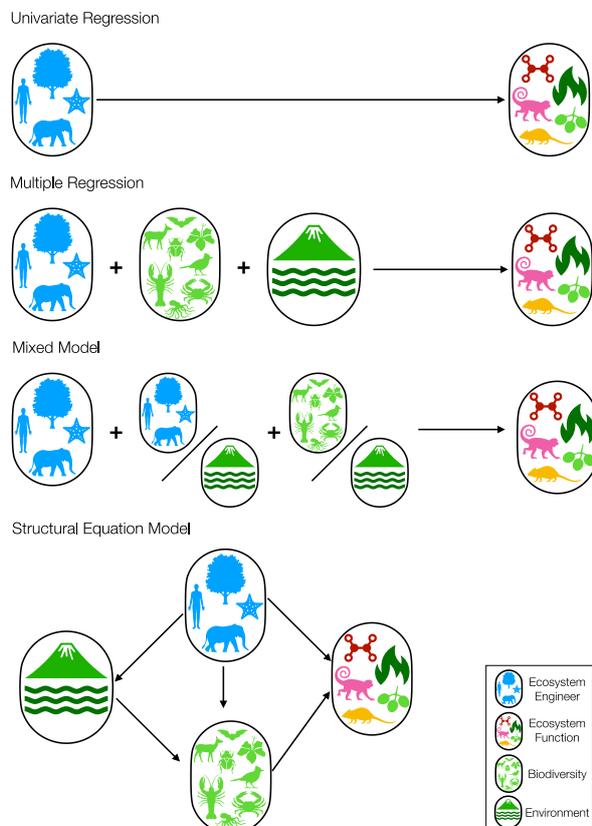

Figure 4 Summary of main causal relationship models sorted in increasing complexity.

Linear regression and mixed models assume direct cause–effects, but relationships between EF and EE as well as between EE and biotic factors can be altered by a third one. That is, chains of direct causal relationships can lead to indirect effects. As such, causal EE–EF relationships can be described by both direct and indirect effects as part of complex causal networks. Structural equation models (SEM) are used to infer causes from observational or experimental data to test or formulate causal hypotheses (Grace 2006). SEM incorporate quantitative information required for explanation, prediction, and mechanistic inference. Overall, they provide parameters, similarly to regression models we described above, that show the magnitude of the direct or indirect effects that a set of independent variables (either observed or latent), exert on EF dependent variables (for full description, see Grace, 2006).

b. Mechanistic explanations

Identifying the mechanisms underlying the influence of EEs on EF allows us a deeper understanding of the processes underlying these effects as well as better predictive ability under unobserved conditions (Bolker 2008). Models of EEs include the biophysical modification of the habitat and key EFs as well as the time scale and temporal legacy of those effects (see Hastings et al., 2007). Mechanistic models should describe a set of related but independent variables where the effects of EE on EE are quantifiable and generalizable across a range of conditions (Soetaert and Herman, 2009). The output of a mechanism will thus vary predictably in response to manipulation of any of the input variables. Mechanistic models express exchanges of energy or mass between ecological variables, usually concentration, biomass, density, frequency, or rate. Here, we synthesise major theoretical progress and mathematical models for the effects of EEs on EF (for a full tractation, see Hastings et al., 2007).

By means of Turing reaction–diffusion morphogenesis equations (Meron, 2007), modelling self-organisation processes highlight the role of EEs in the assembly, dynamic, diversity and stability of ecosystems (Bera et al., 2021). The formation of spatial patterns such as bare soil, spot, rings, strips or uniform vegetation results from a combination of positive and negative feedbacks between EEs and resources at individual and landscape scales (Gilad et al., 2007). As in the case of dry environments, two EEs regulate EF: cyanobacteria create soil crusts, which generate runoff, while shrubs or tussock grasses

create soil mounds, increasing water infiltration, uptake and accumulation of nutrients available to other species. These apparently contrasting EE effects create Turing instability as patches with plants attract more water than soil covered with cyanobacteria, further increasing the growth of those plants and other species in their surroundings as well as supporting the persistence of cyanobacteria soil crust at distant areas. The development and functioning of these engineered environments can be modelled by means of partial differential equation systems representing the three state variables of density of EEs, water runoff, and water infiltration (Gilad et al., 2007; Bera et al., 2021). Furthermore, a lattice, cellular automata model with neighbours' spatial interactions are useful to explicitly include the process of facilitation by EEs (Kefi et al., 2007). Systems of ordinary differential equations shall include local facilitation for colonisation and survival as well as soil degradation and regeneration to understand and predict the stability of vegetation and associated functions.

Animals acting as EEs can also play a role in spatial self-organisation processes that mediate EF. As in the case of ants, ground-nesting termites, and rodents, social-insect colonies and territoriality can generate hexagonal landscape elements like Mima mounds and Namibian fairy circles (Tarnita et al., 2017). The formation of regular patterning influences different EF including soil nutrient content, texture and porosity as well as nitrogen fixation and fungi decomposition. Mechanistic models include identifying first the sources and scale of spatial overdispersion by means of point-pattern analyses (e.g., Ripley's *L* and pair-correlation functions). Analogously to above-mentioned Turing feedbacks, a model of partial differential equations can include interactions between animal territories, vegetation and water flows (Tarnita et al., 2017). Parameters shall include territorial interference, colony establishment, growth, and mortality as well as plant above- and below-ground biomass, soil water uptake and diffusion to predict key EFs such as robustness and resilience against drought.

5. The engineer *par excellence*: *Homo sapiens*

Humans are arguably Earth's greatest ecological engineers — our activities have recently reshaped the biosphere, affecting both biotic and abiotic processes, and resulting in stark consequences for biodiversity and ecosystem functioning (Ellis 2015). Human activities have shaped the biosphere for millennia and touched most terrestrial and aquatic ecosystems

(Ellis et al., 2021; Steffen et al., 2015). Industrial era activities, including widespread land use intensification, globalisation, extractivism and fossil fuel use, and the appropriation of traditionally managed indigenous lands, have particularly negative environmental (and social) impacts (Ellis et al., 2021). On the other hand, the long history of environmental stewardship by indigenous peoples (e.g. Kimmerer, 2015), the importance of biocultural landscapes for conservation, and more recent efforts to restore ecosystems, all highlight the potential for humans to use their engineering capabilities to promote diverse and functional ecosystems (Lewis et al., 2019). While activities related to certain industrial societies and corporations to date have had many negative environmental impacts (e.g., Diaz et al., 2019; Bradshaw et al., 2021), successful conservation and restoration actions, including traditional indigenous practises (e.g. Levis et al., 2017), demonstrate the potential for humans to use their engineering capabilities for enhancing ecosystem functions (Byers et al., 2006). In this section, we discuss how knowledge as well as experimental and modelling approaches from the ecosystem engineer literature can be leveraged for sustaining EF and, at the same time, for biodiversity conservation, ecosystem restoration, and climate change mitigation and adaptation.

Given the urgent need to reverse the current biodiversity crisis, the UN has declared 2021-2030 the UN Decade on Ecosystem Restoration (www.decadeonrestoration.org). Ecological restoration is the process of assisting the recovery of an ecosystem that has been disrupted (SER 2021). Ecosystem restoration encompasses multi-taxa approaches, by ranging from habitat-focused approaches such as reforestation, to trophic rewilding, which is based on animal species reintroductions or use of functionally analogue species to promote EF (Svenning et al., 2016; Oliveira-Santos & Fernandez 2010). Regardless of the methods, intentionally restoring ecosystems is, intrinsically, engineering ecosystems. However, our role as EE in the restoration processes, and the use of different EE species to aid restoration practises, has been seldom explored.

Restoration actions are informed by implicit (and often vague or poorly defined) assumptions that managed species will serve as EEs. For example, tree planting initiatives assume that planted trees by acting as EE will create habitat for biodiversity, sequester carbon, and improve the provisioning of ecosystem services like timber and water. However, tree planting often fails to produce these benefits because trees are planted in inappropriate locations (Coleman et al., 2021; McFadden et al., in review), the wrong tree

species are selected (Coleman et al., 2021), or because planting initiatives inadvertently incentivize tree planting even when it conflicts with their ultimate conservation goals (Heilmayer et al., 2020). We argue that restoration actions could be made more effective by explicitly framing target species as EEs and modelling how they could change the biotic and abiotic environment *a priori*, ultimately improving the desired EF.

EEs and their effects on multiple EFs can easily be incorporated into restoration decision-making using an adaptive management approach (Figure 5). Adaptive management is a structured framework for making natural resource management decisions (Williams 2011). The key steps in this iterative process include problem assessment, planning, implementation, evaluation and adjustment to the original plan. We can extend the classic adaptive management framework to explicitly incorporate ecosystem engineers by deepening the planning phase (Figure 5 steps 2-4) and performing modelling studies of the effects of EEs on the desired EF. By using modelling studies, managers can compare the effects of different management alternatives *in silico* prior to implementing them in the real world. This additional step will likely help reduce costs, streamline restoration projects, and improve their effectiveness.
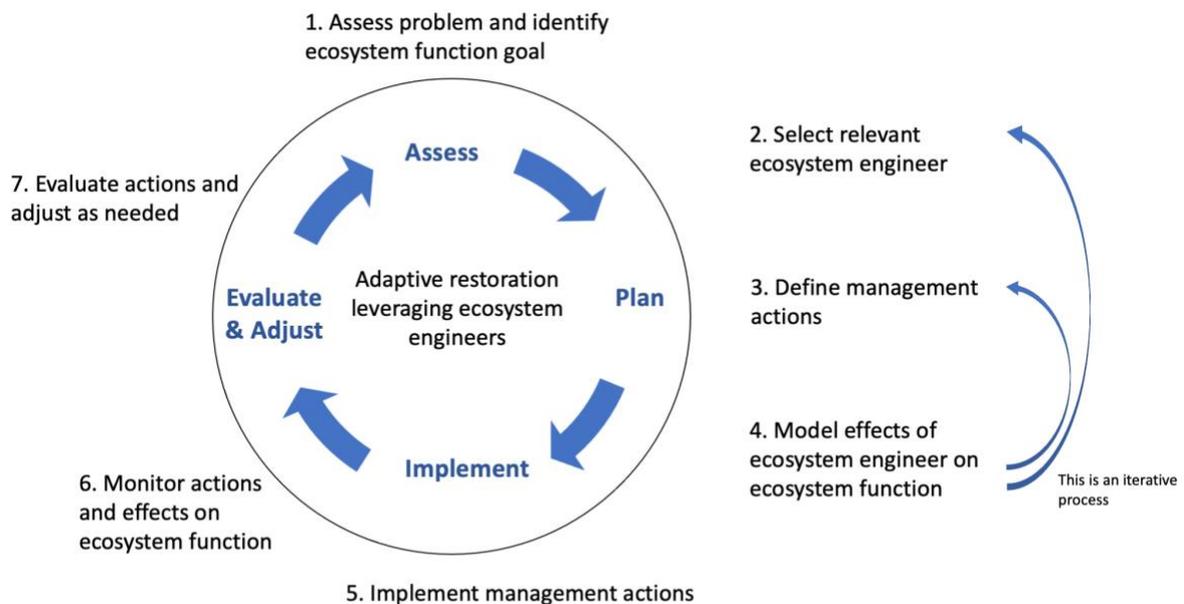

Figure 5. Workflow for incorporating knowledge of ecosystem engineers into restoration decision making.

Modelling the effects of EE reintroductions on EF should consider biotic interactions and abiotic effects of species. Forecasting trophic interactions can be achieved combining species distributions and species interactions in other locations in a probabilistic framework (Marjakangas et al., 2018). Under this framework, species whose reintroduction would promote a higher number of ecological interactions, or more unique interactions, may be prioritized, and species can be appropriately selected based on restoration goals (Genes et al. 2017; Marjakangas et al. 2018). Adding to this approach an abiotic layer that allows the assessment of the effects of each species on their environment, and weighing its effects on different spatial and temporal scales, would allow prioritisation of species with stronger engineering impacts.

In conclusion, the scale and pace of global biodiversity loss today has increasingly highlighted the importance of protecting EFs which support the Earth's biota, including humans. Major restoration efforts such as the UN's Decade on Ecosystem Restoration, Africa's Great Green Wall, or the Blue Nature Alliance, have emphasised society's role in the management of ecological processes. EEs, due to their elevated impact on ecological and biophysical systems, may be a linchpin for these global efforts to maintain healthy, functional ecosystems.

The protection or reintroduction of individual species has already been leveraged by conservationists to aid in ecosystem restoration. The effects of grey wolves (*Canis lupus*) or sea otters (*Enhydra lutra*) on the biodiversity of riparian areas in Yellowstone National Park or the kelp forests of the North Pacific are some of the best known examples of successful management. Yet, despite the potential for trophic interactions such as these to reshape ecosystems, the role of EEs and non-trophic processes remains remarkably unexplored within a restoration context. The conception of humans as engineers within management frameworks is also similarly uncommon.

To explicitly include EEs in restoration programs and generate *a priori* predictions of their effect, it is paramount to be able to accurately describe the relationship between EEs and EF and apply in the appropriate context. Here we have outlined common monitoring, experimental, and modelling techniques for detecting and quantifying EF responses to an EE. We argue that integrating these methods, emphasising the role of EEs, and broadening our conception of *Homo sapiens* as EEs will more effectively and efficiently achieve the targets of existing biodiversity programs and restoration initiatives.

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