

REVIEW

Monitoring and modelling the effects of ecosystem engineers on ecosystem functioning

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Abstract

1. Biodiversity is crucial for supporting ecosystem functioning, yet some species play a disproportionate role in maintaining complex ecological processes. Ecosystem engineers are species that directly influence ecosystems by modifying biophysical environments, creating novel habitats, altering biogeochemical cycles, increasing biodiversity and/or modulating ecological processes. Although these species may substantially influence ecosystem functioning, their role is often overlooked and difficult to quantify. Understanding the status, dynamics and trends of ecosystem engineers is essential for mitigating biodiversity loss and maintaining healthy ecosystems.
2. This review reveals the common but underappreciated roles that ecosystem engineers play in ecosystem functioning across many different taxa, biomes and ecological processes. We first synthesise how knowledge of ecosystem engineering improves our understanding of species interactions and the ecological processes underlying both ecosystem functioning and BEF relationships. We provide a conceptual model for addressing the effects of ecosystem engineers in BEF research and ecological dynamics.
3. We provide a 'how to' analytical framework for monitoring and quantifying changes in ecosystem engineers and their effects on ecosystem functioning. This framework includes (i) what variables to measure, how and at which scale; (ii) experiments involving species exclusion or removal, introduction and comparative designs when experimental manipulation is not feasible and (iii) statistical, data-driven and theory-driven models.
4. We discuss how to leverage ecosystem engineering in the context of current global change and ecosystem restoration efforts. Including ecosystem engineers in conservation and restoration programs, when implemented in the appropriate context and supported by an understanding of ecological mechanisms and processes, may be crucial for sustaining biological diversity and functional ecosystems.

Gianalberto Losapio, Luísa Genes, Christopher J. Knight, Tyler N. McFadden and Lucas Pavan contributed equally to the work.

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anthropocene, biodiversity, conservation, ecosystem engineer, ecosystem functions, habitat-forming species, restoration, species interactions

1 | INTRODUCTION

Biodiversity contributes to ecosystem functioning (EF), economic revenue and human health (Binder et al., 2018; Brandl et al., 2019; Isbell et al., 2022; Kilpatrick et al., 2017). EF includes ecological processes arising from the combined activity of different species such as biomass production, trophic transfer through plants, animals and microorganisms, matter and nutrient cycling, water dynamics, heat mitigation, air regulation, information flows and disease control (de Groot et al., 2002; IPBES, 2019). Yet, some species like ecosystem engineers (EEs) play a disproportionate role in maintaining complex ecological processes, but their impact on EF is often understudied. This knowledge gap limits our ability to predict and anticipate the changes in EF that follow biodiversity change.

Key to solving this problem is the recognition that organisms can 'act' on their surroundings and changing environmental conditions. Species that are particularly impactful at changing their environment are often referred to as EEs (Crain & Bertness, 2006; Wright & Jones, 2006). EEs create microhabitats and alter biophysical conditions that influence other species by modifying niche and resource availability, which drive ecosystem cascades and affect biodiversity, ecological networks and functioning (Coggan et al., 2018; Decker et al., 2019; Gibb et al., 2021; Hastings et al., 2007; Losapio, Norton Hasday, et al., 2021; Odling-Smee et al., 2003; Schöb et al., 2012).

EE impacts occur across different levels of biological organisation and ecological systems (Figure 1), which may have important implications for conservation and restoration efforts (Byers, 2022; Davidson et al., 2012; Desie et al., 2020; O'Brien et al., 2020). Plant and animal EEs create novel microhabitats and are integral in the establishment, survival and reproduction of other species (Lortie et al., 2016; Losapio, Schmid, et al., 2021; O'Brien et al., 2020; Padilla & Pugnaire, 2006; Schöb et al., 2012), which have major implications for EF and human livelihoods that rely on it (Lacher et al., 2019; Mallen-Cooper et al., 2018). The effects of EEs on EF transcend trophic levels and ecosystem boundaries. Hence, the conservation and restoration of EE populations should have direct ecosystem effects. Specifically, EEs should be considered an important component of restoration since reintroducing extirpated EEs may assist in restoring ecosystem functionality (Byers, 2022). Monitoring and modelling of EE populations can, thus, provide insights into levels of EF in the restored ecosystem.

Despite growing consensus on the importance of EEs, the ecological role of EEs in EF and the BEF relationship is poorly understood. One possible reason is that EEs are often viewed as exceptional case studies rather than key drivers of functioning. Likewise, engineering effects are usually thought of as exceptional examples (i.e. beavers) rather than being fairly ubiquitous. While the role of EEs in creating niches and influencing the resources available to other species

In the case study systems of EE facilitating understorey plant species and pollinator community at the same time, positive complementarity effects and neutral to negative selection effects have been observed between EE and understorey plants (Losapio, Schmid, et al., 2021). Thus, it seems that complementarity between EE and other plant species supports higher abundance and diversity of pollinators, most likely facilitating understorey diversity and indirectly widening pollination niches and attractiveness for generalist species. In all, the engineering effect is positive for EF and pollinator service.

Using the framework based on the variance partitioning of biodiversity effects (Loreau & Hector, 2001), it is possible to distinguish between complementarity and selection effects including EE. The framework has been developed in the context of biodiversity experiments involving monocultures and species mixtures and addressing biomass production. Here we adapt these equations to quantify the net biodiversity effect of EE on EF.

Considering EE and associated community (e.g. understorey species) as two distinct functional groups j that can either co-occur (O) or not (A), the diversity effects can be calculated as:

$$\text{Complementarity} = 2 \times \frac{EF_{Aj}}{EF_{Aj}} \times \frac{EF_{Oj}}{EF_{Aj}} - w_j,$$

$$\text{Selection} = 2 \times \text{cov} \left(\frac{EF_{Oj}}{EF_{Aj}} - w_j, EF_{Aj} \right).$$

For complementarity effect, the mean EF provided by both EE and the associated community when they do not co-occur (EF_{Aj}) is multiplied by the mean of the ratio between observed EF for each EE and associated community in the presence of both groups (EF_{Oj}) and in their absence (EF_{Aj}) minus the relative abundance w_j of EE and associated community. This indicates the deviation from average expectation of EF given by neutral interactions between EE and the associated community. The higher the complementarity effect, the higher the positive (direct or indirect) interactions between EE and the associated community. For selection effect, it is taken the covariance between deviation from expectation of EF in the presence of engineering effects on the associated species community and their contribution to EF in the absence of the other group. The higher the selection effect, the higher the single contribution provided by EE or the associated community.

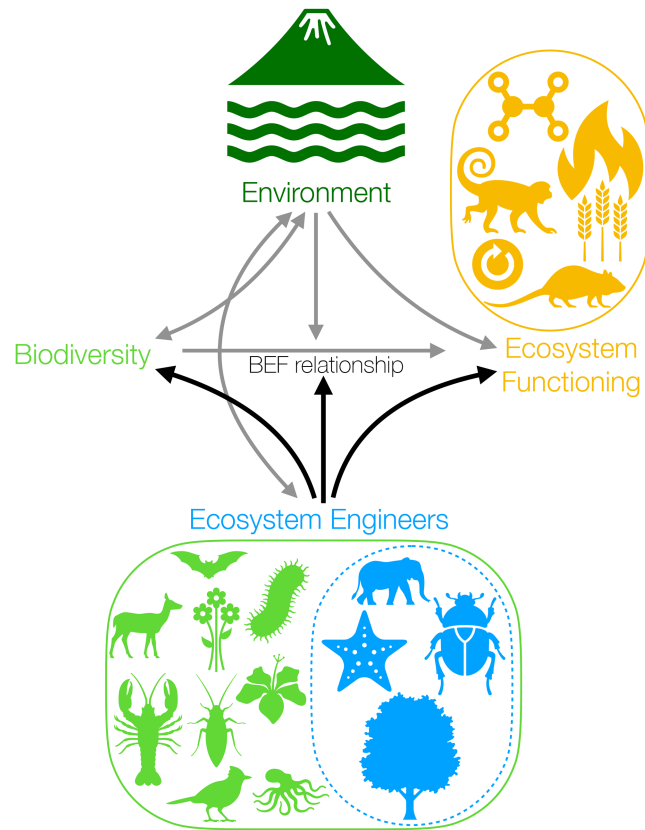


FIGURE 1 Ecosystem engineers mediate complex relationships among the environment, biodiversity and ecosystem functioning. Although ecosystem engineers are part of the overall biodiversity, they are represented separately to emphasise their unique ecological role. Black arrows represent interactions promoted by ecosystem engineers considered in this paper, while grey arrows represent relationships that are outside the scope of this paper.

may be a central driver in EF, it is typically omitted from ecological theory and biodiversity experiments addressing BEF relationships. Additionally, biodiversity conservation programs, monitoring schemes and modelling studies all often overlook key engineering effects on ecological functions (Byers, 2022; Hastings et al., 2007; Kefi et al., 2012). Integrating EE impacts on ecological processes and the mechanisms that increase EF and underlie the BEF relationship, is therefore, highly relevant for advancing ecological theory, modelling and applications (Figure 1). Monitoring the status, changes and trends of EEs is key to understanding and protecting biodiversity while supporting EF.

Here, we highlight the common but underappreciated roles that EEs play in EF across taxa and biomes. We first provide an integrative view of how knowledge of ecosystem engineering effects would improve our understanding of species interactions and ecological processes supporting EF. We provide a conceptual and empirical model for addressing the role of EEs in driving the BEF relationship. Then, we synthesise approaches, methodologies and analytical frameworks for monitoring and modelling how EEs influence EF. Finally, we highlight a road map for mainstreaming the inclusion of EE in EF research and biodiversity conservation.

2 | ECOSYSTEM ENGINEERING EFFECTS AND THE BEF RELATIONSHIP

The global decline of biodiversity and the erosion of EF are among the most crucial contemporary challenges facing humanity (Dirzo et al., 2014; Isbell et al., 2022). Beyond accelerated rates of biodiversity loss, the local-to-global extinction of EEs may especially threaten healthy EF and the well-being of humans that rely on it (Bradshaw et al., 2021; Davidson et al., 2012; Díaz et al., 2019). To address such challenges, it is crucial to direct efforts towards understanding, monitoring and modelling the ecological functions of EEs. Not only for the maintenance of EF directly but also for the maintenance of biodiversity on which many EF rely. This may inform ecosystem management to support and restore the effects EEs have on EF (Byers, 2022; Davidson et al., 2012; Palmer et al., 2020).

Biodiversity experiments have already yielded important insights into the consequences of biodiversity loss for EF (Bongers et al., 2021; Huang et al., 2018; Isbell et al., 2022; Tilman et al., 2014). For instance, species-rich communities provide higher levels of functioning than monocultures because different species can better complement each other (complementarity effect) and because biologically diverse communities are more likely than monocultures to include species with the highest levels of functioning (selection effect) (Hooper et al., 2005; Loreau & Hector, 2001; Schmid et al., 2002; Tilman et al., 2014). However, the mechanisms responsible for those positive impacts of diversity remain unknown. This may be due in part to the difficulty of including EEs in controlled BEF experiments. Because EE's influence both EF and biodiversity, they may be particularly relevant for understanding how complementarity and selection effects drive the BEF relationship. Here, we identified three main pathways whereby EEs support EF and influence the BEF relationship (Figure 1): (i) maintaining biodiversity, (ii) increasing EF and (iii) mediating the BEF relationship itself.

First, EEs may support biodiversity through diverse mechanisms (Losapio, Schmid, et al., 2021). For example, through the biogenic formation and maintenance of microhabitats that facilitate associated species (Davidson et al., 2012; Schöb et al., 2012). Such facilitation increases biodiversity at both local and landscape scales (Bulleri et al., 2018; Cavieres et al., 2014; Crain & Bertness, 2006; Thomsen et al., 2018). Therefore, the persistence of different species due to EEs would ultimately strengthen the positive effects of biodiversity on functioning.

Second, EEs directly increase EF via their presence and activity. For example, among animals, digging mammals (e.g. *Lagostomus maximus*, *Bettongia lesueur*) and beavers (*Castor* spp.) generate geophysical disturbance; trampling megaherbivores (e.g. *Ceratotherium simum*, *Loxodonta africana*) enrich soil fertility, decrease pathogens and reshape landscape connectivity; and social insects (e.g. *Odontotermes montanus*, *Syntermes dirus*) enhance microorganism activity and biogeochemical cycling (Coverdale et al., 2016; Davidson et al., 2012; Dirzo et al., 2014;

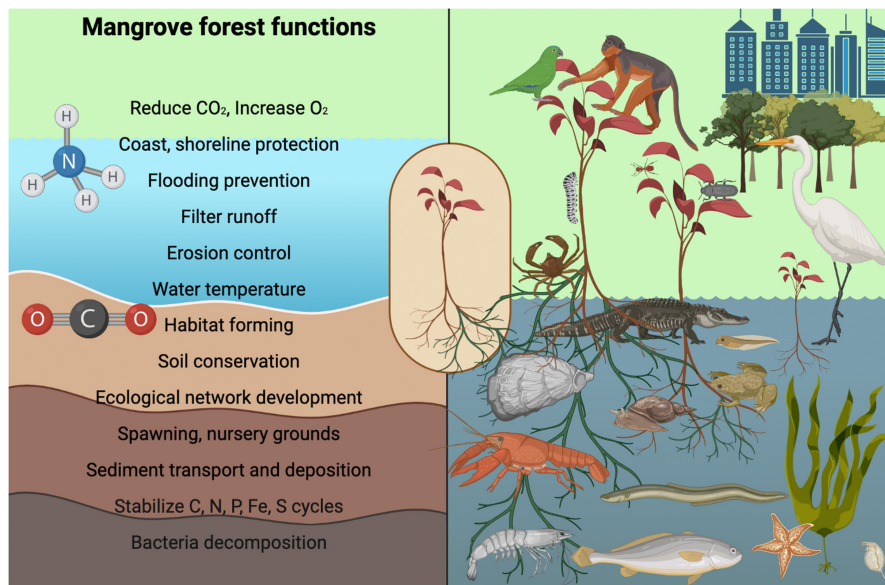


FIGURE 2 Mangroves are tropical intertidal forested wetlands that play a key role in nutrient cycling, carbon storage, habitat provisioning and shoreline protection. By occurring at the interface of terrestrial, marine and freshwater ecosystems, mangroves support substantial biodiversity and cross-ecosystem linkages, facilitating commercially important marine fishes and large colonies of nesting waterbirds.

Tarnita et al., 2017; Wright & Jones, 2006). This is also the case for cushion plants (e.g. *Arenaria tetraquetra*, *Azorella* spp.), sea-grass (*Posidonia oceanica*, *Zostera capricorni*), woody plants such as mangroves (e.g. *Avicennia marina*; Figure 2) and leguminous shrubs (e.g. *Retama sphaerocarpa*) that provide microhabitats for multiple trophic levels, host mutualistic partners, ameliorate microclimate conditions and increase water availability (Callaway, 2007; Padilla & Pugnaire, 2006). The resulting reduction of environmental constraints enhances EF. Consequently, such engineering effects should be considered when addressing the mechanisms of the BEF relationship and for gaining multiple ecological benefits at once.

A single EE species can provide multiple functions simultaneously, as illustrated by the case of mangrove forests (Figure 2). Mangroves shape coastal geomorphology through the production of organic matter and the retention of mineral sediment, thereby supporting soil accumulation, the development of deep organic soils and adaptation to sea level rise (Figure 2). Monitoring mangrove growth and quantifying their engineering effects is, therefore, crucial for successful biodiversity maintenance and ecosystem management.

Lastly, EEs may also mediate the relationship between biodiversity and EF. In the context of BEF studies, the contribution of each species to functioning is measured as species performance along a single niche axis (Loreau & Hector, 2001; Schmid et al., 2002). Analogously, the contribution of EEs to BEF can be examined by using measures of ecosystem engineering effects that influence EF (see Box 1). For their biophysical impact on the environment and ecological significance, EEs may be considered as a unique functional group that mediates and strengthens the BEF relationship by contributing to both complementarity and selection effects. Addressing the relative importance of complementarity and selection effects due to EEs would inform the ecological processes underlying positive BEF relationships and help support functional ecosystems. In the following box, we provide an analytical framework for addressing the diverse effects of EE on the BEF relationship.

Next, we provide a synthesis for developing models addressing the EE effects on EF and BEF relationship. Given context dependencies, we focus on the challenge of uncovering general patterns and promoting cross-system understanding. We end by providing suggestions for leveraging EEs in a conservation and restoration context.

3 | MONITORING ECOSYSTEM ENGINEERS AND ECOSYSTEM FUNCTIONING

Developing robust models of EE impact on EF requires understanding the mechanisms involved in engineering effects and the degree of biodiversity and ecosystem change. This requires monitoring 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. The main components of monitoring programs must address what to measure, where and how (Walters & 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.

3.1 | Study goal and which variables to measure

When examining the relationship between EEs and EF, 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.

If the study does not already entail specific EEs or functions, first we need to ask: which species may act as EEs? And, which functions may they affect? Then, we need to consider the direction and magnitude of that effect: is the EE causing increases or decreases in functioning 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 and proximate causes of the engineering effects we are observing?

Appropriate variables to measure include one or more explanatory variables representing EE impact and one or more response variables representing the functions of interest. Both EE explanatory variables and EF response must be clearly defined, reliably measurable, quantifiable and based on the appropriate scale of biological organisation. Here, we focus on monitoring changes in population-, community- and landscape-scale metrics. The choice of the variable to measure (Table S11) is often driven by feasibility, which varies between EEs and systems.

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 and 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.

3.2 | Biological contexts and spatiotemporal scales

Having chosen the state variables to be measured, we then need to monitor and understand where and when that change occurs. While we redirect the reader to general literature addressing ecological (Lindenmayer et al., 2013; Lindenmayer & Likens, 2010), ecosystem (Eyre et al., 2011; Sparrow et al., 2020) and biodiversity (Pereira et al., 2013; Walters & Scholes, 2017) monitoring frameworks, we present here a synthetic guidance for monitoring EEs and EF effects across ecological and spatiotemporal scales.

Spatiotemporal and biological scale may strongly influence the selection of relevant explanatory (EE) and response (EF) variables (Gonzalez et al., 2020). First, consider potential explanatory variables, in this case, a quantifiable change in some EE. Then, determine the biological scale on which potential EEs mediate or modify a function of interest. For example, if a single species directly participates in the provisioning of a function, the biological scale is narrow. In these cases, it may be appropriate to incorporate explanatory variables that quantify measures of individuals (e.g. body condition,

survival, reproductive output) (Fløjgaard et al., 2017). In studies where the focal function is mediated by a multitude of species interactions occurring simultaneously, the biological scale is broader. Then, explanatory variables that consider community-level metrics such as species richness and composition are often employed.

While biological scale is key for determining suitable explanatory variables, spatiotemporal scale is often important for selecting reasonable response variables. Once measures of an EE are selected as potential modifiers of a function, the main focus then becomes being able to detect those changes (i.e. selecting a scale on 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 spatiotemporal scale on which changes in functioning 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 function itself can also determine this scale of observability. Non-linear relationships between EE and function 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 evaluating the relationship between EE and functioning.

EEs may have variable effects on functioning 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). The 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 function, 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 they act as damaging invasive species in their exotic range in southern South America. Despite these different roles and perceptions, beavers in North and South America have similar engineering 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-engineered ecosystems are novel, native species may not be

adapted to beavers, and engineering effects of beavers are less socially desirable (Anderson et al., 2009). As conservation is a value-driven process, while an EE can have positive effects on EF, yet it may pose undesirable socio-ecological impacts.

3.3 | Experimenting

We can experimentally test the role of EEs by manipulating EEs (i.e. considering EEs as the treatment) and measuring the resulting impacts on EF. Although inferring causal relationships and quantifying effects does not always 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 functioning. We identified three broad possible experimental manipulation types: (i) exclusion or removal, (ii) addition or reintroduction and (iii) comparative, semi-experimental designs 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. In the sections below, we highlight common and useful approaches used in EE experimental manipulations. This is not intended as an exhaustive review but rather as a synthesis of the main approaches.

Exclusion methods are usually adopted for mobile EEs (animals) while removal methods are used for sessile ones (plants and microorganisms). Fences that exclude large mammal EEs from the ecosystem provide opportunities to examine the relationships between wildlife loss (i.e. defaunation) and different functions, including productivity, fire suppression and disease regulation (Dirzo et al., 2014). 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). An example of long-term exclusion provided by the Mpala Research Centre in Kenya (Young et al., 2014) indicates that losing EE increases the risk for zoonotic diseases.

Excluding smaller EEs like soil and marine macrofauna usually takes place at fine spatial scales (on the 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 *Spartina densiflora* by arbuscular mycorrhizal fungi, indicating that crabs mediate species interactions and in doing so modulate EF such as biomass productivity.

Excluding or removing EEs or manipulating their abundance are experimental approaches to quantify how much EF depends on EE. A treatment where EE is absent would also reveal the consequences of EE loss or extinction. Translocating EE species is an effective way of examining their impact on abiotic and biotic processes involved in EF, as found in studies using species reintroductions (Bos et al., 2007; Layton et al., 2019; Shelamoff et al., 2019). For example, translocating different treatments of marine kelps that vary in area size and

density and measuring kelp growth, survival and abiotic conditions under each treatment. In this case, 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 (Layton et al., 2019). In a similar way, transplanting canopy-forming kelp *Ecklonia radiata* in artificial reefs demonstrated how this EE increases the diversity of other plant and animal species (Shelamoff et al., 2019). Measuring and monitoring light infiltration as well as turfing algae suppression is crucial to reveal how kelp EE facilitates critical species such as reef-forming oysters *Ostrea angasi* and supports the whole functioning of the ecosystem. These experiments also highlight a case of EE intra-specific and interspecific facilitation, a possible mechanism by which EE strengthens the BEF relationship.

Finally, comparative designs that use data across temporal or spatial treatments can be employed to examine the influence of EEs on EF when the addition or removal of an EE has already occurred (e.g. species invasions or extirpations) or if the addition or removal is logistically, environmentally or ethically unfeasible (protected species and areas). 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. Combination of long-term monitoring (15-year' time-series data of kelp forest) and structural equation modelling demonstrated not only that EE biomass is positively associated with biodiversity and EF but also that EE mediates this relationship by shading out understory algae that would otherwise compete with sessile invertebrates (Miller et al., 2018). This combination of comparative designs with modelling provides stronger mechanistic inference, as we discuss further in the following section.

4 | MODELLING

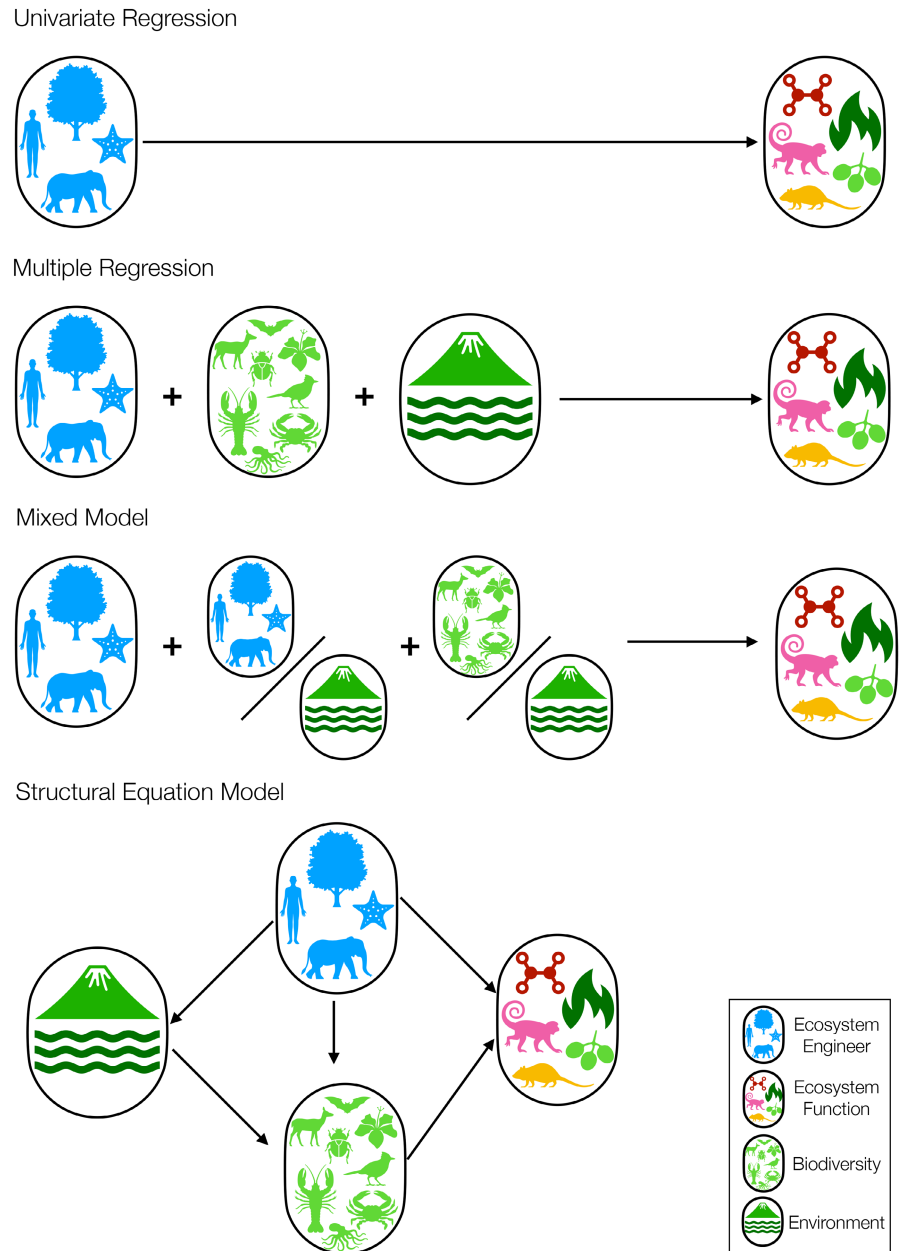
Modelling the effects of EEs on EF serves the purpose of determining scientific explanations for observed relationships, anticipating changes in EE and EF and enabling predictions and scenarios. This requires integrating aspects of both causal and mechanistic perspectives.

4.1 | Causal relationships

Identifying causal relationships is a necessary step to formulating mechanistic explanations of ecological processes underlying the effects of EE on EF. A series of steps are required for the formulation of such ecological pathways (Figure 1).

The first one is to establish simple, dependency relationships without consideration of the mechanism involved in the connection between EE and functioning such as pollination or productivity (Figure 3). This means addressing what will happen to EF if EE changes or remains stable or to quantify whether specific changes in EEs influence EF. We can use the general form of $Y = F(X)$, where

FIGURE 3 Summary of main causal relationship models that can be used to devise the effect of EE on EF, sorted in increasing complexity.



EF Y responds to EEs X . A simple model to parametrize this relationship is a univariate linear regression, such as $Y = \alpha + \beta X + \epsilon$, with $\epsilon \sim N(0, \sigma^2)$. Here, α is the mean value of EF in the absence of EE, whereas β is the parameter of main interest indicating the magnitude of the effects of EE on EF. Parametrizing this model (i.e. inferring estimates of α and β with confidence intervals) will tell us the average level of EF in the absence of EEs (α) as well as how much EF increases or decreases with EE (β). The term ϵ is the associated, compound error that includes measurement accuracy and precision and unaccounted population variability associated with third factors. This error is assumed to be normally distributed with mean 0 and variance σ^2 . The parameters of this model can be estimated using a least squares approach, by a maximum likelihood estimation procedure, or MCMC methods (for an in-depth discussion, see Bolker, 2008; Gotelli & Ellison, 2012; Zuur et al., 2009).

Although such a simple univariate linear 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 are the climatic, biogeographical and historical background, spatial and temporal scales, 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 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 , that are relevant to understanding and predicting the effects of EE on the EF (Figure 3). For instance, pollination is influenced by the combination of EE density (X_1) and plant

diversity in the understory (X_2). Although EE and diversity alone can explain part of the variation observed in pollination diversity regardless of each other, the effects of EE are stronger at low rather than high diversity (Losapio, Norton Hasday, et al., 2021). The model needs to account for both the additive effects of EE and plant diversity as well as the dependency of EE effects on diversity. By including the statistical interaction between EE and diversity, the model is formulated as $Y = \alpha + \beta_1 X_1 + \beta_2 X_2 + \varepsilon$, where β_1 and β_2 indicate the strength of the relationships between EF and EE and diversity, respectively. This way, one can test how EE affects the BEF relationship: the interaction parameter $\beta_1 \cdot \beta_2$ will indicate how the effects of diversity on EF change with EE. A positive term would indicate that EEs strengthen the BEF relationship, a negative term that EEs and biodiversity have antagonistic effects on EF, while a non-significant term indicates that EEs have no effects on the way biodiversity shapes EF.

Research and monitoring programs often involve large, complex and multiscale designs spanning different communities, sites and regions (see e.g. Walters & Scholes, 2017). EF studies often involve many blocks or transects for different EEs, habitats and sometimes biomes. Measurements taken according to such a hierarchical, multilevel structure led to nested data (Zuur et al., 2009). Monitoring schemes often measure the same EE individuals, populations or communities over time, producing time-series data. They include environmental and biotic variables that are measured at different resolutions and scales and have biological replicates that are correlated spatially or individually, such as when EF is measured in the same site before and after the exclusion or reintroduction of EEs. Furthermore, statistical replicates may be heterogeneous (e.g. high variation within EE populations or different EE genotypes), paired, grouped or 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 cannot handle error terms ε that are heterogeneous hierarchical data with observations that are not independent (Bolker, 2008). Thus, linear regression models must be replaced with mixed modelling.

Generalised mixed models (i.e. hierarchical linear models or multilevel models) better support the analysis of EE-EF relationship in those cases of repeated measurements, random effects, hierarchical structure, heterogeneous variance or spatiotemporal correlation (Zuur et al., 2009). Mixed models consist of a fixed term and a random term, such that $Y = F(X, Z)$, where EF is the response variable and EEs together with other 'environmental' factors are the fixed term X and constitute a random term Z . While the fixed term is identical to a linear regression, with the predictor variables X_i as described above, Z contains components that allow to model EE species identity and composition, variance heterogeneity, nested data, temporal correlation, spatial correlation and random noise. Here, we briefly summarise the main components of biodiversity and EF monitoring schemes, and for a deeper traction, we redirect the reader to specialised literature (see e.g. Bolker, 2008; Gotelli & Ellison, 2012; Zuur et al., 2009).

There are no strict rules for considering EE species as fixed or random terms, but the choice depends on the aim of the study and the type of data. If the aim is to generalise the engineering effects over many different EE species, then EE identity can be used as a random term. Instead, if the aim is to compare the engineering effects among different EE species, then EE identity should be used as a fixed term. Furthermore, intrinsic variability across EEs populations and habitats may lead to heterogeneity of variance as in the case of high variability in abundance, density or productivity among EE and associated species.

To allow for 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 $\varepsilon \sim N(0, \times \sigma^2_j)$. As the effects of EE on EF may vary within biomes and across habitats, it is important 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 $y_{ijk} = \alpha + a_k + a_{ijk} + (\beta_1 + b_k + b_{ijk}) X_1 + \varepsilon_{ijk} + \varepsilon_k + \varepsilon_{ijk}$ where y_{ijk} is the EF value measured at i^{th} plot for each habitat j within each biome k .

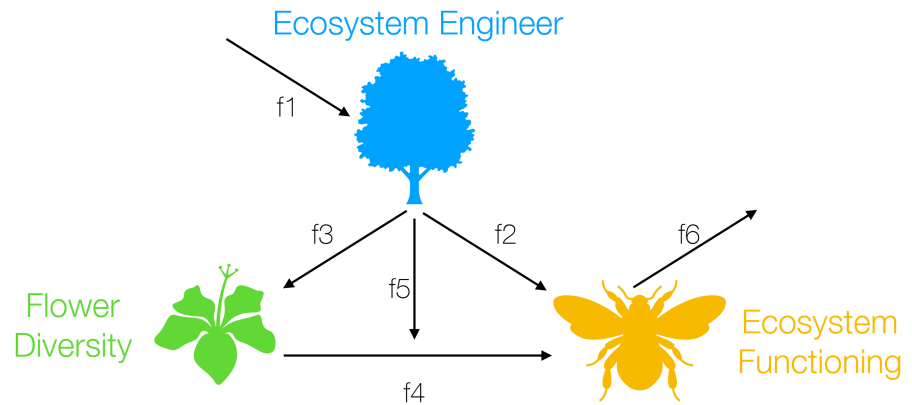
Finally, including a temporal or spatial residual correlation structure into the model allows residuals from different time or space point to covary. For example, when microclimate amelioration is monitored automatically across time in different sites. This is accomplished by modelling $\text{cor}(\varepsilon)$, a correlation matrix for residuals that includes a specific correlation function, such as an 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.

Linear regression and mixed models assume direct cause-effects, but chains of direct causal relationships can lead to indirect effects between EE and EF (Figure 1). As such, causal engineering-functioning relationships can be described by both direct and indirect effects as part of complex causal networks (Figure 4). To this end, structural equation model (SEM) is used to infer causes from observational or experimental data to test or formulate causal hypotheses (for full description, see Grace, 2006). SEMs incorporate quantitative information required for explanation, prediction and mechanistic inference. Overall, they provide parameters, like regression models we described above, that show the magnitude of the direct or indirect effects that a set of EE variables exert on EF-dependent variables. Furthermore, different measurements can be combined into composite, latent variables to provide a more compelling picture. This way, one can elucidate whether the EE directly increases EF via its presence and activity or whether such effect is mediated by a third species.

4.2 | Mechanistic models

Identifying the mechanisms underlying the influence of EEs on EF allows us a deeper understanding of the ecological processes and provides better predictive ability under unobserved conditions. Models

FIGURE 4 Flowchart of the SUP (Shrub, Understorey, Pollinator) model. Leguminous shrubs act as EE facilitating understorey plant diversity and increasing EF provided by pollinators via microhabitat creation. Functional groups are connected by ecological functions (arrows).



of EEs include the biophysical modification of the habitat and key EFs (for a full treatment of the topic, see Hastings et al., 2007). Mechanistic models describe a set of related but independent variables where the effects of engineers on functioning are quantifiable and generalizable across a range of conditions (Soetaert & Herman, 2009). Following the modelling approach proposed by Kefi and colleagues (Kefi et al., 2012), the effects of EE on biodiversity, EF and BEF relationship can be modelled using functional classes that are parameterized according to ecological interactions and associated mechanisms.

We consider the simple Shrub, Understorey, Pollinator (SUP) model where leguminous shrubs acting as EE increase EF both directly via their presence and indirectly by supporting biodiversity and BEF relationships (Figure 4). This SUP model represents a restored semi-arid environment where EEs have been planted to support EF and restoration. The model unit is biomass density. All else being equal, the change over time of the three S-U-P components result from ecological interactions as:

$$\frac{dS}{dt} = f1 - f2 - f3 - f5,$$

$$\frac{dU}{dt} = f3 - f4,$$

$$\frac{dP}{dt} = f2 + f4 + f5 - f6.$$

Ecological interactions between S-U-P components are represented as ecological functions: f1 is net EE survival due to restoration; f2 is pollen and nectar uptake from EE; f3 is growth of understorey species; f4 is pollen and nectar uptake from understorey flowers; f5 is net facilitation-inhibition balance of understorey pollination; f6 is pollen transfer and honey production (Figure 4). These functions f_i are directly dependent on the biomass of EE and all other component species. Each function can be expressed mathematically considering any parameter that could affect the ecological interactions between the components including, for instance, germination rate, maximum pollinator visitation rate, maximum pollen uptake and pollen transport efficiency. The simplicity and generality of such an SUP model is that the dynamic of specific components is the result of the sum of all inflows minus all outflows. Here, additional population parameters (assumed to be constant) that are not

explicitly modelled such as basal metabolism, respiration, mortality and reproduction can be added or subtracted from the basic model.

By means of Turing reaction-diffusion morphogenesis equations (Cuddington et al., 2007), modelling self-organisation processes can highlight the role of EEs in the assembly, dynamic, diversity and stability of ecosystems and EF (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 feedback 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 plant patches 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 (Bera et al., 2021; Gilad et al., 2007). Furthermore, a lattice, cellular automata model with neighbours' spatial interactions is useful to explicitly include the process of facilitation by EEs (Kefi et al., 2007). Systems of ordinary differential equations should 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 the above-mentioned Turing feedback, a model of partial differential equations can include interactions between

animal territories, vegetation and water flows (Tarnita et al., 2017). Parameters should 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.

Ultimately, mechanistic models provide a deeper understanding of ecological processes underlying EE and EF relationships. This approach allows modellers to transfer knowledge and predictions to data-poor but analogous environmental contexts.

5 | OUTLOOK

Human activities have shaped the biosphere for millennia and touched most terrestrial and aquatic ecosystems (Ellis et al., 2021; Steffen et al., 2015). Yet, industrial era activities, including widespread land-use intensification, globalisation, extractivism and fossil fuel use, pollution and the appropriation of traditionally managed indigenous lands, have disproportionate negative environmental and social impacts (Ellis et al., 2021). While activities related to natural resources exploitation have had many negative environmental impacts (Bradshaw et al., 2021; Díaz et al., 2019), successful conservation and restoration actions, traditional indigenous practices (Levis et al., 2017) and environmental stewardship (Kimmerer, 2015) highlight the potential for humans to use their capabilities to promote diverse and functional ecosystems (Lewis et al., 2019). In this section, we discuss how ecological knowledge as well as experimental and modelling approaches from the EE literature can be leveraged for sustaining EF and, at the same time, for biodiversity conservation and ecosystem restoration.

Ecological restoration is the process of assisting the recovery of an ecosystem that has been disrupted. Ecosystem restoration ranges from habitat-focused approaches such as reforestation, to trophic rewilding, which is based on animal species reintroductions or the use of functionally analogue species to promote EF (Oliveira-Santos & Fernandez, 2010; Svenning et al., 2016). Restoration actions are often informed by implicit assumptions that managed species will serve as EEs. This is particularly the case for forest ecosystems (Figure 5), where the engineering effects and biodiversity effects are often intermingled. For example, mangrove restoration initiatives assume that planted trees will create habitat for biodiversity, sequester carbon, support multiple EF and improve the provisioning of ecosystem services like timber and water (Figure 2). 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.

The protection and reintroduction of individual mammal species have already been leveraged by conservationists to aid in ecosystem restoration. The effects of grey wolves *Canis lupus* or sea otters *Enhydra lutra* on biodiversity and EF 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.

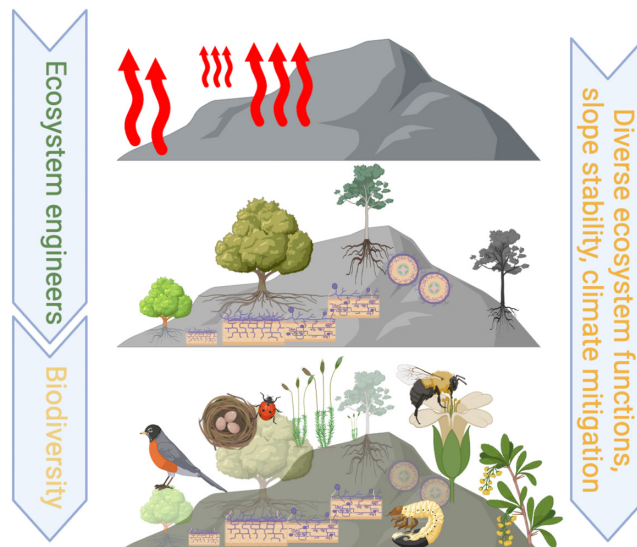


FIGURE 5 Ecosystem restoration should focus more on improving ecological processes. Addressing the effects of ecosystem engineers on multiple ecosystem functions would help restore not only the structure of the ecosystem but also its functionality. We postulate that engineering effects prevail in the first phase of restoration, while biodiversity effects become more important with the proceeding of the ecological succession.

Yet, the role of EEs and associated non-trophic engineering effects remain remarkably unexplored within a restoration context (Bird & Nimmo, 2018).

As we have seen, EEs play a disproportionate role in EF as compared to non-engineering species, reshaping ecosystems, driving community dynamics and supporting biogeochemical cycling. Given their crucial functions in diverse ecological processes, we hypothesise that engineering effects prevail during the first phase of the restoration process and ecological succession, whereas diversity effects become more important with time. This hypothesis is consistent with the fact that plants EE are often those stress-resistant species that thrive when most other species lose. Considering this pattern in the context of ecological cascades triggered by EEs, EEs may be seen as the primers of community dynamics underlying the ecosystem restoration pathways (Figure 5).

Here, we hypothesise that considering EEs early in restoration may be an effective prioritisation strategy in systems that are heavily reliant on EEs for EF. We suggest that restoring EE species can initiate long chains of ecological interactions that support EF and ecosystem recovery (Figure 5). To test this hypothesis and develop effective conservation strategies, restoration actions should monitor the status and dynamics of EE and quantify their effects on EF. Knowledge of these changes and trends should inform subsequent interventions.

EEs and their effects on multiple EFs can easily be incorporated into restoration decision-making using an adaptive management approach. 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 EEs by deepening the planning phase 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.

Modelling the effects of EE reintroductions on EF should consider biotic interactions and abiotic effects of species. Forecasting trophic interactions can be achieved by combining species distributions and species interactions in other locations in a probabilistic framework (Coggan et al., 2018; Gibb et al., 2021; Marjakangas et al., 2018). Under this framework, species that would promote a higher number of ecological interactions, or more unique interactions, may be prioritised, 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 engineering effects of each species on their environment, would allow prioritisation of species with stronger engineering impacts.

In conclusion, the scale and pace of global biodiversity loss today have increasingly highlighted the importance of protecting EEs that support the Earth's biota, including humans. Major restoration efforts such as the launching of the United Nations 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 functional ecosystems. To explicitly include EEs in restoration programs and generate a priori predictions of their effects, it is paramount to be able to understand the interactions between EEs and EF and apply them in the appropriate context.

AUTHOR CONTRIBUTIONS

All co-authors contributed equally to the conception of the study, acquisition and synthesis of literature, drafting the article and making the figures.

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CONFLICT OF INTEREST STATEMENT

The authors have declared no competing interest.

DATA AVAILABILITY STATEMENT

No data were used or produced for this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S11: Key measurements of plant and animal ecosystem engineers.

Table S12: Summary of ecosystem engineer species and related ecosystem functions that are often measured and their scale.

Table S13: Ecological functions provided by ecosystem engineers that need to be monitored.

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