Ecosystem engineers shape ecological network structure and stability: A framework and literature review

Dirk Sanders, Enric Frago

Received: 10 February 2023 | Accepted: 31 May 2024

DOI: 10.1111/1365-2435.14608

Functional Ecology BRITISH ECOLOGICAL SOCIETY

REVIEW

Ecosystem engineers shape ecological network structure and stability: A framework and literature review

Dirk Sanders[1] | Enric Frago[2]

[1]Centre for Ecology & Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn, Cornwall, UK

[2]CIRAD, CBGP-Centre for Biology and Management of Populations, Montpellier, France

Correspondence
Dirk Sanders
Email: d.sanders@exeter.ac.uk

Funding information
Biotechnology and Biological Sciences Research Council, Grant/Award Number: BB/X010473/1; Agence Nationale de la Recherche

Handling Editor: Maria Briones

Abstract

1. Ecosystem engineering is a ubiquitous process where species influence the physical environment and thereby structure ecological communities. However, there has been little effort to synthesize or predict how ecosystem engineering may impact the structure and stability of interaction networks.
2. To assess current scientific understanding of ecosystem engineering impacts via habitat forming, habitat modification and bioturbation on interaction networks/food webs, we reviewed the literature covering marine, freshwater and terrestrial food webs, plant-pollinator networks and theory.
3. We provide a conceptual framework and identify three major pathways of engineering impact on networks through changes in resource availability and energy flow, habitat heterogeneity and environmental filtering. These three processes often work in concert and most studies report that engineering increases species richness. This is particularly marked for engineers that increase habitat heterogeneity and thereby the number of available niches.
4. The response of network structure to ecosystem engineering varies, however some patterns emerge from this review. Engineered habitat heterogeneity leads to a higher number of links between species in the networks and increases link density. Connectance can be negatively or positively affected by ecosystem engineer impact, depending on the engineering pathway and the engineer impact of species richness.
5. We discuss how ecosystem engineers can stabilize or destabilize communities through the changes in niche space, diversity, network structure and the dependency on the engineering impact. Theory and empirical evidence need to inform each other to better integrate ecosystem engineering and ecological networks. A mechanistic understanding how ecosystem engineering traits shape interactions networks and their stability will be important to predict species extinctions and can provide crucial information for conservation and ecosystem restoration.

KEYWORDS
ecological communities, ecosystem functions, habitat modification, physical environment, restoration, species interactions

1 | INTRODUCTION

Ecosystem engineers or habitat modifiers are species that impact the physical environment through their activity or presence (Hastings et al., 2007; Jones et al., 1994; Largaespada et al., 2012). The concept of ecosystem engineering is linked to "niche construction". This term is used by evolutionary biologists to describe how the metabolism, activities and behaviour of organisms modify environmental states and ultimately impact eco-evolutionary dynamics (Boogert et al., 2006; Laland et al., 2015). Engineer impacts on the physical environment can be thought of as operating on three, non-exclusive pathways by altering abiotic conditions (e.g. temperature, pH, wind or sediment deposition), consumable abiotic resources (such as trapping of run-off water and distribution of nutrients) or non-trophic resources (living space, enemy free or mutualist rich space) (Figure 1, Sanders et al., 2014). The pathways can overlap with respect to the organisms, for example, light can be a resource for a plant and a condition for a predator.

A meta-analysis reported that engineering effects by animals increase habitat heterogeneity—and thereby lead to higher organismal diversity (Romero et al., 2015) with a similar positive effect uncovered for nurse plants (Arredondo-Núñez et al., 2009). Heterogeneity and diversity are enhanced by many typical habitat formers or foundation species that create new habitats for other organisms such as corals providing calcium carbonate structures, beavers building dams, or kelp and nurse plants buffering harsh conditions (Coggan et al., 2018). Often more subtle engineering effects are provided by habitat modifying engineers, for example when insects create galls (Barbosa et al., 2019) or mammals leave footprints that are subsequently used by other species (Baruzzi & Krofel, 2017). Engineering

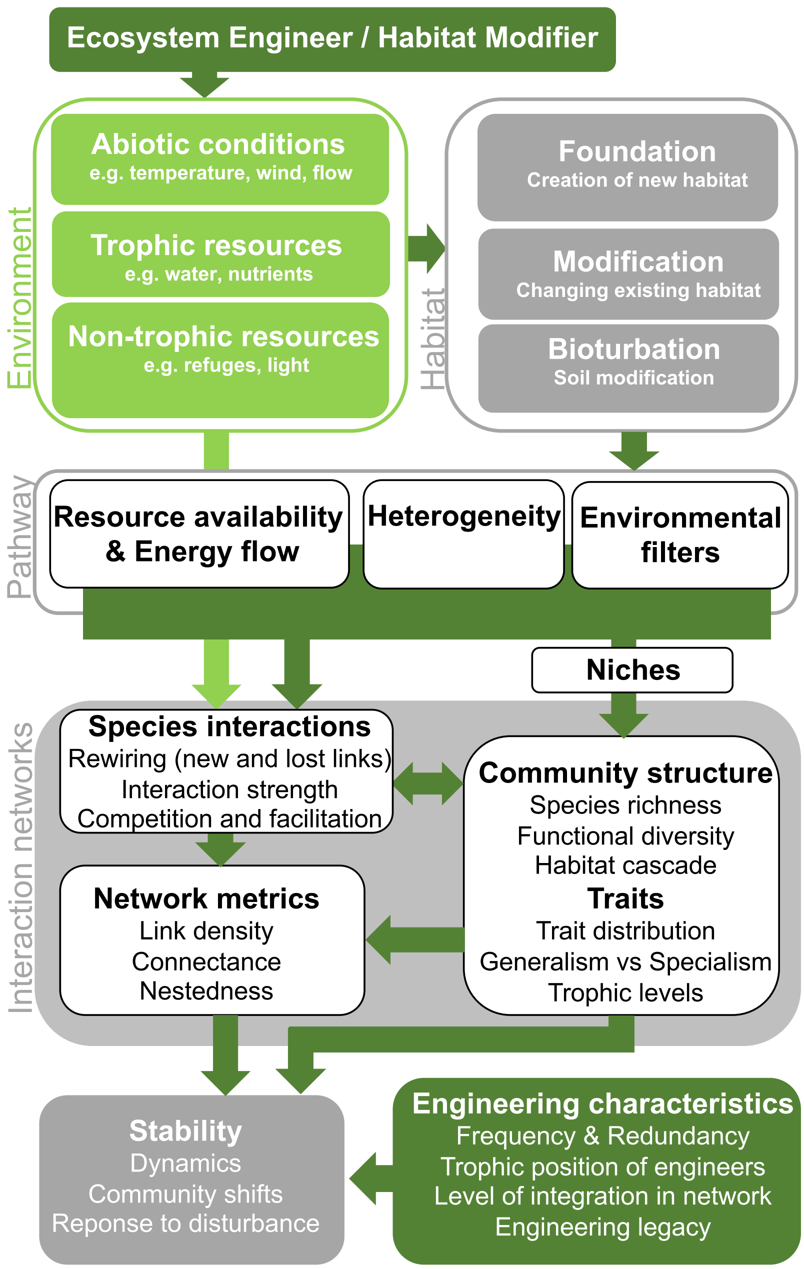

FIGURE 1 Conceptual framework linking ecosystem engineering to interaction network structure and stability. Ecosystem engineers impact habitats as foundation species, habitat modifiers or through bioturbation by changing the physical environment (abiotic conditions, trophic resources and non-trophic resources). We identify three major pathways how ecosystem engineers impact interaction networks and community structure: resource availability and energy flow, habitat heterogeneity and environmental filters. The creation of a more heterogeneous habitat can increase the number of niches. Changes to network structures and engineering characteristics have consequences for the stability of these communities.

often occurs through bioturbation too, which describes the modification of soils and sediments and can be considered as a special mechanism of habitat modification (Romero et al., 2015). Strong or subtle, ecosystem engineering is likely to play a key role in many ecological systems as it can be considered as the most prevalent non-trophic interaction between species (Sanders et al., 2014). With such ubiquitous effects in mind, ecosystem engineering changes many species interactions either directly between the engineer and other species (e.g. by cutting down perches for predatory birds, voles reduce their own predation risk through engineering Zhong et al., 2022), or through modulation of interactions between other species in the network (e.g. Nummi et al., 2021). Within ecological interaction networks, the impact of engineering species showcase how direct and indirect trophic species interactions are often coupled with non-trophic interactions (e.g. Estes & Duggins, 1995; Thomas et al., 2009).

A recent study clearly demonstrates the interplay between trophic and engineering effects in driving food web interactions. The invasive big-headed ant (*Pheidole megacephala*) controls major biophysical structure across landscapes in Kenya by disrupting the mutualism between native ants and the dominant whistling-thorn tree (Kamaru et al., 2024). This makes these trees vulnerable to elephant browsing, resulting in landscapes with much higher visibility. As a result, lions become less successful in preying on zebras and switch to African buffalo. To better understand how species interact in nature, such organism—environment interactions and their eco-evolutionary feedback need to be integrated into community and network ecology (Kéfi et al., 2015, 2016; Sanders et al., 2014). Ecosystem engineering can alter interactions ranging from facilitation to antagonism, and the extent of the effect can vary from simply modulating a link between two species, to alter whole ecosystems. For example, foundation species have a marked impact on ecological communities because their arrival and settlement in an ecosystem generate habitats that allow the subsequent establishment and persistence of new species thus creating novel communities (Ellison et al., 2005). While the concept of ecosystem engineering is often used to describe the consequences that keystone or foundation species have on diversity patters, less research has been devoted to understanding the resulting network structure and its stability.

Such an approach is crucial to understand tightly interwoven networks of species and their interaction with the abiotic environment, both of which are changed by human impact. This understanding will help to estimate the potential for cascading effects following the loss or invasion of engineering species and will ultimately help determine stability measures such as ecosystem resistance and resilience to perturbations. Multilayer networks have been used to map different types of species interactions such as trophic and mutualistic (Pilosof et al., 2017), but studies that have considered ecosystem engineering (or habitat modification) at the network level are still very limited (but e.g. Kéfi et al., 2015; Olff et al., 2009; van der Zee et al., 2016). Therefore, here we use a literature review to synthesize existing knowledge into a conceptual framework (Figure 1). Based on this current scientific understanding, we conceptualize and review major pathways by which ecosystem engineering alters the structure of interaction networks. We then discuss the consequences of engineering impact for community stability.

2 | ENGINEERING ALTERS NETWORK STRUCTURE

Interaction networks describe complex assemblages of interacting species. As such they have become a crucial tool for modern community ecology to study natural systems and their response to human impact. To allow the comparison of different types of networks, network structure or topology can be measured with metrics (Montoya et al., 2006).

To link engineering impact to network or food web responses, we searched the literature using a set of search strings in Web of Science (see Appendix S1). We only included primary research that measured the response of the community or network structure to the impact of an engineer species, resulting in 36 studies (with two studies reporting each two separate engineer impact cases). For each study, we extracted information about engineer identity, whether it was native or exotic, the community/food web/network, the engineer classification (habitat forming, habitat modification, bioturbation as classified by Romero et al., 2015), the main outcomes for diversity and the structure of the network or food web, such as network metric(s) and functional composition that have been measured (Figure 2). A list of the studies and the extracted data are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.z34tmpgnw).

Most studies were conducted in aquatic environments (16 marine 2 and freshwater), which was followed by terrestrial food webs (11), plant-pollinator networks (3), and four extra studies, two on microbial communities and another two using theory. The main documented engineers were habitat formers with 23 cases, 12 performing habitat structural modifications, and 3 bioturbation (Figure 2). Thirty-six cases provided data about the impact of ecosystem engineering on diversity. In 27 cases, the authors reported increased species richness in the engineered habitat compared to controls without the engineer. Three studies found a negative impact on diversity, one study a variable effect, and five studies reported no changes. We found information about network or food web structure responses in 32 cases (Figure 2). These include link density (network degree), connectance (the proportion of realized links in the web), centrality (quantifies the extent to which species are central to the network in term of number of links) and nestedness (the degree to which specialist are using a subset of interactions provided by more generalist species). Studies also reported functional richness and changes to predator trophic levels (biomass and richness).

Based on the variety of network/food web level responses reported in the literature (see Figure 2), we conceptualize and review pathways by which engineering affects ecological interaction networks. We suggest three major pathways: (i) resource availability and changes to energy flow in the system, (ii) habitat heterogeneity

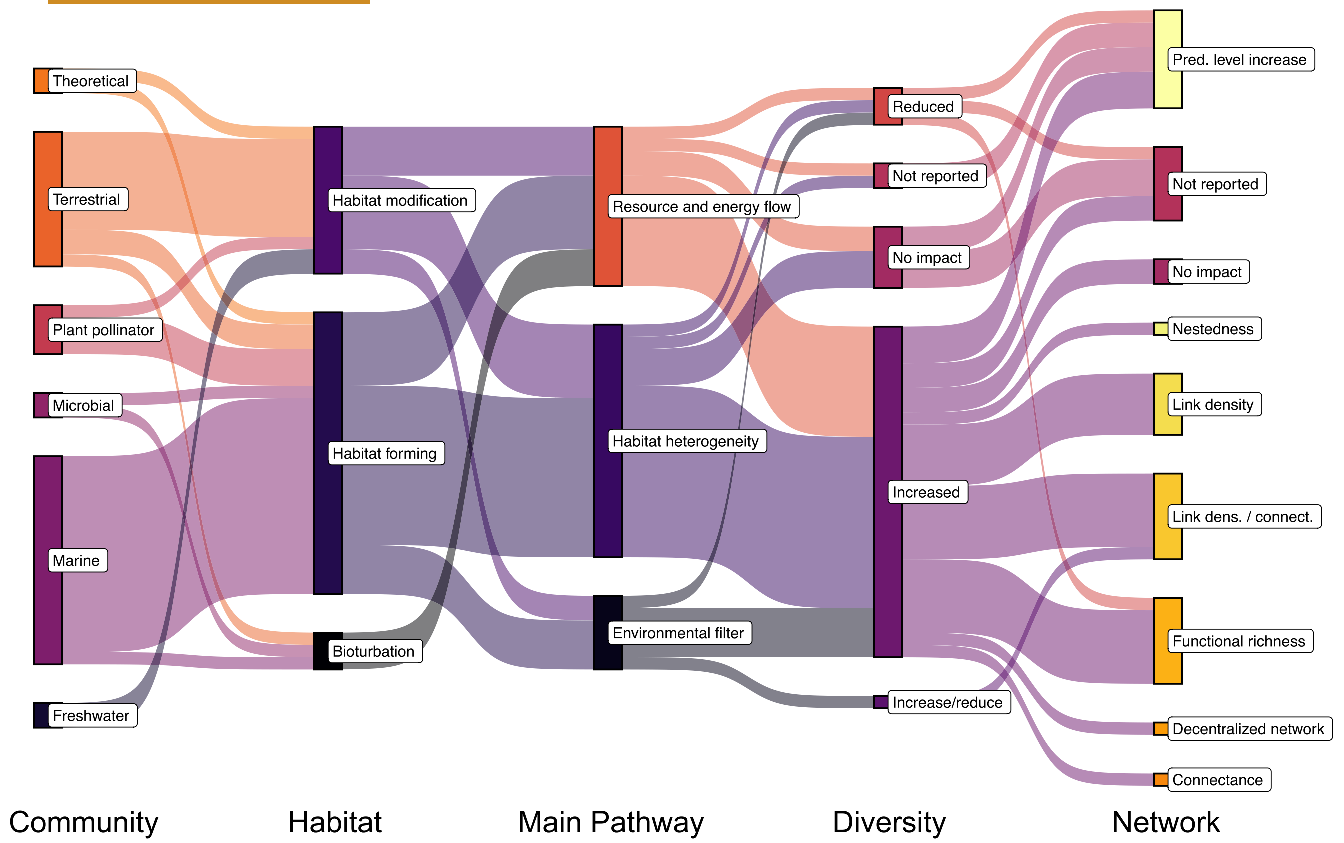

FIGURE 2 Sankey flow diagram showing the number of studies included in this review that investigate the impact of ecosystem engineering on interaction networks and the information flow between different categories. Categories include community types (based on main marine and terrestrial biomes), the type of habitat impact by the engineering species, the main engineering pathway for each case, and the engineering effect on diversity and network metrics. The data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.z34tmpgnw.

and (iii) environmental filters (Figures 1 and 2). Most engineering impacts reported here represent a combination of those processes but often we can identify the main pathway that leads to major changes in diversity and network structure of engineered communities.

2.1 | Resource availability and energy flow

Ecosystem engineers can concentrate or dilute abiotic resources, such as water and minerals (Jones et al., 2010), or organic matter (e.g. Law et al., 2016). Some species such as benthic invertebrate shredders (Moore, 2006), earthworms (Eisenhauer, 2010) or crabs (Kristensen, 2008) do so through increased decomposition rates of litter via physical fragmentation and bioturbation in sediments and soil. Examples of engineers influencing resources also include the trapping and storage of dust, litter, detritus or water mostly by both terrestrial and aquatic plants (Cheng et al., 2021; Graham, 2004; Hoffman et al., 2016; Law et al., 2016). Controlling resource availability can be considered as an environmental filter pathway (if this drives survival through the species' fundamental niche) or as changing or redirecting the flow of energy thereby boosting certain food chains or trophic levels. The change in resource distributions can lead to a net increase or decrease in the availability of mineral nutrients and a long-term increase or decrease in primary production via node modulation at the base of the food web (Sanders et al., 2014).

In most cases, engineering effects through resource availability increase diversity with consequences for network metrics, with overall little evidence for a negative impact on diversity (Figure 2). However, dams created by beavers are a good example of how engineers can alter resource availability and energy flows through habitat forming and modification, with often negative effects on the local diversity. Beaver-induced changes to stream morphology change how freshwater resources are distributed throughout the river's course with important consequences for macroinvertebrate communities, which in turn affect dependent food webs and ecosystem functions. North American beavers (*Castor canadensis*) were introduced to Tierra del Fuego Island in 1946 for their fur and have spread onto the South American mainland. A study by Anderson and Rosemond (2010) indicate that invasive beaver's engineering activities resulted in greater flows of terrestrial organic matter subsidies to in-stream food webs. In beaver-modified sites, flows of terrestrially derived organic matter (amorphous detritus, leaves and wood) to secondary consumers in the benthic food webs were substantially enhanced. As a result of the engineering, food web structure was simplified in beaver ponds with only two of the five possible functional groups contributed >1% of total organic matter flow in ponds (but see the discussion of positive beaver effects on diversity at a larger spatial scale below). Through this effect, beavers can increase the connection between aquatic and terrestrial food webs as found by Nummi et al. (2011) who reported larger bat abundances on flowages where beavers were present. Such changes to stream macroinvertebrate communities and their cascading effects suggest that recolonization of beavers across North America and as exotic species in other parts of the world may be profoundly altering stream functioning and food webs.

Several examples of ecosystem engineers altering flows of resources and energy come from marine ecosystems whereby reef-forming species capture sediments and both organic and inorganic matter to create novel ecosystems and trophic networks. Such filter feeders tend to have a marked impact on the energy flows in a system by removing nutrients from the water column and making these available for benthic communities (e.g. Christianen et al., 2017). Two examples from our literature review involve the tube-building worm *Lanice conchilega*, which transfers carbon and organic matter from the water column into seabed trophic webs thereby increasing the energy flow through the food web substantially. The presence of this species triggers dramatic shifts in macrofaunal species composition and network structure with a higher number of links but lower connectance (De Smet et al., 2016), even if a study using stable isotopes revealed that basic trophic metrics remained unaltered by the presence of the worm (De Smet et al., 2015).

Bioturbation effects on ecological communities tend to act through changes in resource availability and energy flow. An example of this pattern comes from a report by Sanders and van Veen (2011) who studied the impact of ant colony presence within grassland food webs. They found that through bioturbation in and around their mounts, ants increased the abundance of main decomposer and herbivore groups which then resulted in higher abundance and diversity of spiders as main generalist predators. This positive bottom-up cascade through engineering was counteracted of ants also acting as generalist predators. Another example highlights the strong impact of bioturbation on the redirection of energy flow in food webs. The non-native polychaete worm *Marenzelleria arctia* invaded Baltic Sea benthic environments becoming a dominant ecosystem engineer in many areas. This species modifies the physical, chemical and biological characteristics of bottom sediments through bioturbation and bioirrigation (flushing of worm burrows with water) and stimulate the decomposition of organic matter by worms and microorganisms. *M. artica* has a marked impact on the energy flow in the system moving resources away from the main food web including macroinvertebrates and fish to a new offshoot food chain. This food chain does not provide energy transfer from autochthonous and allochthonous organic matter to the upper trophic levels and as a consequence negatively affects fish abundances (Golubkov et al., 2021).

Engineering and trophic impacts are often intertwined. Two studies highlight how ecosystem engineer species can provide habitat, while also driving nutrient availability as engineers and trophic resources resulting in highly diverse habitats. The giant kelp *Macrocystis pyrifera* is creating highly diverse kelp forests primarily through the provision of energy and habitat (Graham, 2004). Kelp forests in North America are dominated by *Macrocystis pyrifera*, a brown algae species that can grow to more than 40 m and alter current flow and velocity, sediment deposition and sediment stabilization. This important engineer creates one of the most productive and diverse marine ecosystems. Kelp forests are the backbone of these ecosystems, and their disappearance leads to low diversity, species-poor barrens (Rogers-Bennett & Catton, 2019). By comparing the food webs of kelp forests with areas of localized giant kelp deforestation, the author of this report concluded that many species were found exclusively in forested areas. Most of these associations were clearly identified as trophic and/or structural associations with giant kelp itself, but kelp acted as a source of fixed carbon for other producers through either direct grazing or the production of phytodetritus. Primary, secondary and tertiary consumer levels therefore increased in density and diversity. With deforestation, the source of primary production shifts from primarily kelps to ephemeral microalgae, macroalgae and phytoplankton. Archer et al. (2020) studied the impact of reef-building sponges providing structure and capturing large amounts of carbon from the water column as foundation species on food web structure. These sponges too have a dual role as ecosystem engineers and being at the base of the food web they enable. In their study, several metrics of food web topology (e.g. connectance and link density) increased when sponge cover reached a certain threshold. Below this threshold consumers relied on fewer sources and were consumed by fewer predators, resulting in food webs that were more clustered (higher number of subnetworks) and less connected. Above the threshold, food webs were less clustered and more connected, with primary consumers becoming more generalist while at the same time having more predators.

The impact through the modification of resource availability and energy flow can markedly restructure communities (e.g. both above- and below-ground communities, see St. John et al., 2012), often with significant changes to consumer assemblages, interaction strength and network structure (Jones et al., 2021). Engineers can redirect energy flows, either increasing or decreasing resources for primary and secondary consumers. This can trigger bottom-up cascading effects, often leading to major changes at higher trophic levels (e.g. predator diversity and biomass). Further, asymmetries in productivity and turnover rates between energy channels in food webs can increase community stability driven by the behaviour of consumers switching between food web channels (Rooney et al., 2006). Because many engineers affect energy flows and productivity, they may well control heterogeneity of distinct energy channels with differential dynamic properties and hence food web stability (Sanders et al., 2014). Controlling resource availability may also have knock-on effect on communities via productivity—diversity relationships, which can have different shapes ranging from neutral to negative and positive depending on the system and the spatial scale that is investigated (Brun et al., 2019; Craven et al., 2020).

2.2 | Habitat heterogeneity

Habitat heterogeneity and amount are two important factors promoting biodiversity (Heidrich et al., 2020) with concomitant effects on the formation of ecological interaction networks. Habitat heterogeneity and structural complexity usually promotes species richness by providing a larger range of niches as abiotic conditions (also see environmental filters), refuges and resources become more diverse. These conditions allow more species to coexist, reduce extinction risk and ultimately promote speciation (Stein et al., 2014). However, evidence of negative or neutral effects of habitat diversity on species diversity exist (e.g. different groups in Heidrich et al., 2020). This is likely due to a trade-off between habitat amount and heterogeneity. Below a certain threshold of a required habitat type, species are less likely to persist because resource quality also decreases and critical resources may be lacking (Samways et al., 2010). Ecosystem engineers may alter habitat heterogeneity by providing novel habitats thus diversifying the available niche space in a particular ecosystem, while they may also increase habitat amount by expanding an already available ecological niche. This means that we can expect a strong positive effect of the engineer on richness at the landscape scale when the quality or quantity of engineered patches support species that could not survive otherwise. In a literature review, Crooks (2002) suggests that the heterogeneity–niches relationship can be used to predict the impact of exotic engineers: if they increase habitat complexity or heterogeneity they tend to cause abundances and/or species richness to rise (e.g. Davoult et al., 2017), while those that decrease complexity tend to have the reverse effect.

The creation of habitat heterogeneity is a main driver for engineer impact on the structure of ecological networks (Figure 2). Two studies explicitly manipulated structural complexity artificially, which allowed to test for the effect without any confounding factors. Adding artificial structure in the form of wire constructs increased spider predation and biomass (Miyashita & Takada, 2007) while artificial reefs changed networks compared to bare controls (Nauta et al., 2023). In the latter study, species richness (+76%), link density (the number of interactions per species; +15%) and the fraction of basal species (species of lowest trophic level; +40%) was increased, but the artificial reef lowered network connectance by 33%. The effects on food web structure increased over time with a higher species richness (+22%) and more complex food web (link density +13%) on the artificial reef 2.5 years after deployment compared to 1.5 years (Nauta et al., 2023). In other studies, authors estimate network metrics in natural habitats with or without engineering species with similar outcomes for species richness and network complexity. The most commonly used measure was link density (Figure 2), which tends to increase in engineered habitats, indicating that species have access to more resources and resources are exposed to a higher diversity of consumers. For example, van der Zee et al. (2016) measured links per species and network connectance along a gradient of natural habitat restoration from bare habitats to established communities in two coastal ecosystems, a seagrass meadow and saltmarsh habitat. The engineering effect was provided by foundation plants (e.g. *Spartina alterniflora*) that settle in bare soils, and by stabilizing the substrate and through shading allow the settlement of many other species. Even if in this example the engineer alters resource availability and energy flows too, the main impact on networks was through increased heterogeneity. Un-engineered habitats had low species richness, whereas the succession of engineering species settlement led to communities with several plant species and associated herbivores. The authors found that the increase in engineering species concomitantly increased the number of trophic interactions and link density (i.e. the number of interactions per species), while network connectance decreased. The latter effect of decreased connectance is likely the result of increased diversity because small networks harbour a higher proportion of generalists so that species interact more tightly.

Several studies focus on how heterogeneity brought by ecosystem engineers alter specific interactions like competition or facilitation between species. These studies are important because they point to engineering altering specific links within networks and allow for a mechanistic understanding of engineer species as modulators of network structure. It has been shown that engineering can promote biodiversity by providing habitats where poor competitors can escape competitive exclusion (Liautaud et al., 2020). Beaver dams, for example, increase habitat heterogeneity by creating variability along the river flow and in the nearby terrestrial ecosystems (Naiman et al., 1986; Stringer & Gaywood, 2016). The heterogeneity created by such dams can alter network structure, for example by changing the balance in competitive strength between species. This has been shown for the ducks *Anas platyrhynchos* and *A. penelope* (Nummi & Pöysä, 1997) and the sandpipers *Tringa ochropus* and *Actitis hypoleucos* (Nummi et al., 2021): in each pair, the inferior competitor becoming dominant in the presence of beaver dams. Habitat engineers that create heterogeneity through novel structures can also alter trophic networks (Jankowska et al., 2019; Jones et al., 2021) and functional diversity (Jankowska & Włodarska-Kowalczuk, 2022). The provision of refuges can increase or decrease consumer pressure over resources (e.g. Orwin et al., 2016), depending on who benefits. The beetle *Elaphidion mimeticum* creates holes on mangrove trees that can be subsequently used as refuges by mangrove tree crabs, *Aratus pisonii*, leading to an increase in crab herbivory on mangrove plants (Griffen et al., 2017). Gall forming species on plants often provide shelter for natural enemies, thereby increasing top-town control. Galls produced by the nematode *Ditylenchus* increased the abundance of predatory and parasitic arthropods with consequences for herbivore suppression (Pereira et al., 2021). Wetzel et al. (2016) suggested that spiders use galls produced by the wasp *Andricus quercuscalifornicus* as refuges, which led to changes in the composition of herbivore populations on the studied trees. By experimentally removing galls (structures that provide habitat for aphids) made by the psyllid *Baccharopelma dracunculifoliae*, Barbosa et al. (2019) demonstrated that galls had a negative effect on parasitism of the psyllid, but the effect was modulated by aphid inquilines inhabiting abandoned galls. Engineering can also provide refuges for prey, which then reduces consumer-prey interaction strength with potential beneficial impacts on prey diversity (Alvarez-Filip et al., 2011). Increased engineered habitat structure can support prey, increase the flow of energy to higher trophic levels, and thereby increasing predator richness (Wyckhuys et al., 2017) or predator biomass and body size (Breviglieri et al., 2019) and food chain length (Duarte et al., 2015). Therefore, engineering physical complexity and heterogeneity are likely to modify the way species interact with consequences for species persistence in the community.

Some studies report the dependency of community structure on the amount of engineered habitat and demonstrate changes in network structure along gradients of ecosystem engineer density. In these studies, the engineering effect becomes apparent only above a certain threshold in the density of the engineering species. Examples include variations in ecosystem engineer density across the distributional ranges of engineering species (Alvarez-Filip et al., 2011; Archer et al., 2020; Jankowska et al., 2019) or part of eradication programs to remove invasive engineering species (e.g. Siple & Donahue, 2013). Despite the trade-off between habitat amount and heterogeneity for sustaining biodiversity, most studies included here report a positive effect mainly through the heterogeneity pathway. The responses through increased species richness, tends to lead to higher network complexity in these studies in terms of increased link density and higher functional richness.

2.3 | Environmental filter

The environmental filtering concept recognizes that not all organisms will be able to successfully establish and persist in all abiotic conditions (Kraft et al., 2015). Therefore, the environment is acting as a selective force, excluding species from habitats that don't meet the requirements for survival, that is the conditions are outside their fundamental niche. Environmental filtering is considered to be important for explaining community assembly, and, for example, has been shown to drive island species–area relationships through an increased variety of environmental filters in larger islands (Liu et al., 2020). By modifying abiotic conditions, ecosystem engineers can control environmental filtering. Some engineer species add strong filters, e.g. changing soil acidity and other properties to outcompete other species (Osunkoya & Perrett, 2011), while others allow the establishment of certain species. Classic examples of environmental filtering by engineers come from nurse and foundation plants (Filazzola & Lortie, 2014), which attenuate external physical stressors thereby creating suitable habitats for other species and facilitate their establishment. Wilson and Peltzer (2021), reported that both grasses and woody plants engineer soils by changing the availability of water and nitrogen through positive feedback loops, which can lead to the exclusion of the other group. Grasses thus change soil properties to prevent colonization by woody plants, but once woody plants invade similar positive loops allow their expansion. Such engineering effects are therefore key to understand changes in facilitation and competitive interactions in plant communities, and ultimately state changes from grasslands to woodlands. A study by Rogers-Bennett and Catton (2019) showed that filtering through shading can have facilitative effects. By exposing a total of 46 grassland species to different levels of shading, and by measuring their growth after 10 weeks, the authors of this study found that reducing daylight at 50% significantly increased overall plant biomass and benefited a large proportion of the plants studied. However, this engineering effect has also been show to exclude plants (Callaway, 2007), therefore being a powerful factor in driving plant communities.

Initial impacts through environmental filtering on plant communities can further restructure the wider network of species interactions. For example, foundation plants can impact plant-pollinator networks (Losapio, Norton Hasday, et al., 2021). These foundation species engineer soils and increase shading ultimately promoting the settlement of other plant species that provide rich mutualist habitats thereby leading to an increase in some network metrics such as generalism in plants and pollinators, network nestedness and overall diversity (Losapio, Schmid, et al., 2021). The experimental addition of the Mediterranean bush *Cistus albidus*, which can influence plant communities as nurse shrub (Gómez-Aparicio et al., 2004), to local plant communities, increased both plant and pollinator diversity leading to a more nested and generalist plant-pollinator network (Hernández-Castellano et al., 2020).

Significant changes to environmental conditions can reduce species abundance, exclude species completely and simplify food webs. Washko et al. (2020) quantified differences in the macroinvertebrate community between unaltered segments of streams and within beaver ponds in north-eastern Utah. They suggest that the main changes to the environment are finer sediments and lower oxygen levels in beaver ponds. Relative to lotic reaches, beaver pond communities had 25% fewer species, 75% fewer individuals and 90% lower total macroinvertebrate biomass. There were distinct shifts in functional feeding groups too, with beaver ponds containing mainly engulfers such as caddisflies and Chironomidae larvae, whereas lotic reaches contained more scrapers, filterers, and gatherers. Engineers can expand the range of abiotic conditions and allow novel species to establish and restructure existing food webs. Christianen et al. (2017) show the marked impact of shellfish reefs on food web structure by modifying hydrodynamics and sediment grain size. These changes in abiotic conditions (and environmental filters) led to shellfish reefs having consistently higher link density values and top predator abundances, while both connectance and the richness of intermediate species was lower. Species richness (+42%), species density (+79%) and total biomass of benthos, fish and birds (+41%) was also higher on shellfish reefs. These examples show that the impact of engineers through environmental filters on networks is likely mediated by the strength and spatial distribution of those filters. Strong and widespread filters that exclude the majority of species may lead to simplified networks while a mosaic of environmental conditions and filters may lead to increased diversity and network complexity at the landscape level. As we discussed in the previous sections, the different pathways by which engineers impact networks are often intertwined. Environmental filtering is possibly the pathway most difficult to assess in isolation because it often acts in combination with habitat heterogeneity.

2.4 | Synergies and trade-offs between engineering and network structure

The finding that positive effects of ecosystem engineering on diversity were generally linked to increased network complexity, suggest that ecosystem engineering via all three pathways can be an important driver of network structure (Figure 1). An important element to consider when studying such effects is the scale at which ecosystem engineers impact them. At the local level, engineers can switch habitat conditions and reduce local diversity (e.g. Schlatter et al., 2019), but at the landscape scale they may trigger dramatic diversity gains. Beaver ponds can harbour simplified communities (Washko et al., 2020), but at the larger scale, each dam allows the settlement of few new species thus increasing the overall pool of species in a given ecosystem (Wright et al., 2002).

As discussed in the framework by Sanders et al. (2014) changes to the environment can impact networks via node and link modulation, and affecting various proportions and parts of the network. For example, Baiser et al. (2013) found in their food web simulations, that the trophic position of the species that were facilitated by the foundation species had important consequences for food web structure and stability. When only basal species (e.g. plants) were facilitated, the resultant food webs were complex, species-rich and robust to foundation species removals. In contrast, when higher trophic levels (consumer species) were facilitated, the food webs turned out species-poor with low complexity (e.g. connectance) and low robustness. So far, we lack empirical evidence for these stark difference in outcomes, however theoretical models can be essential to provide clear testable hypotheses. Many examples included in this review studied the impact of habitat forming species, which are clearly crucial for the community of that habitat allowing for the coexistence of a wider range of species and increase the complexity of interaction networks. These outcomes are in agreement with the results of a meta-analysis providing strong evidence of positive engineering effects by animal species on diversity in general (Romero et al., 2015).

An important element for the persistence of engineer populations (and thereby the continuous provision of the engineering impact) is their trophic control by natural enemies. Such trophic control of ecosystem engineering can cascade over multiple trophic levels. A clear example comes from kelp forests in which the shift from diverse forests to barrens is often triggered through top-down pressure when sea urchins, the main consumers of *M. pyrifera*, become very abundant (Tegner & Dayton, 2000). In this ecosystem, another layer of top-down control comes into play when urchin outbreaks are controlled by sea otters or disease (Smith et al., 2009, 2021). A similar example comes from ants predating on termites. Dead wood is an important sink for carbon, a source of organic matter in the soil that ultimately alters plant communities. By accelerating this transition, wood-decomposing termites engineer soils, sometimes to a greater extent than microbes (Franklin et al., 1987). By feeding on termites, predatory ants can regulate their populations, and as a consequence alter wood decomposition, soil mineralization and ultimately the dynamics of plant and herbivorous communities (Tuma et al., 2020). All the above examples demonstrate the interconnectivity of trophic and engineering interactions and their combined importance for key ecosystem processes Complex interactions between engineering and feeding impacts can arise leading to unexpected overall net impacts. Zhong et al. (2021) found that plants obtained resources from soil minerals that were made available by ant bioturbation and are consumed by herbivores. This study showed that while herbivory had strong effects on plant biomass, this loss was fully offset by ant engineering soil resources (through burrowing and aeration of the soil) that allowed plants to reallocate biomass to lost parts. A similar offsetting effect was found in another study in which burrows created by Australian digging mammals had a positive effect on scorpions through provisioning of breeding sites, but at the same time burrows reduced the prey availability for scorpions (Gibb et al., 2021). While engineering and trophic effects of the engineer on the community work in different directions, such effects can also be aligned as shown with kangaroo rats with both engineering and non-engineering increasing local diversity (Prugh & Brashares, 2012). While these studies provide us with insights into the importance of ecosystem engineering for the dynamics of natural systems, we need to develop a mechanistic understanding of the positive and negative impacts by different ecosystem engineers, single and combined with different engineering pathways and magnitude.

3 | ECOSYSTEM ENGINEERING AND ECOLOGICAL STABILITY

Ecological stability is a multidimensional concept that aims to capture many non-independent aspects of ecosystem dynamics including temporal and spatial variability, compositional turnover, invasions, and the responses to perturbations (i.e. resistance, resilience and recovery; Donohue et al., 2013, 2016; Xu et al., 2022). While rarely explored in this context, ecosystem engineers are central to many aspects of stability. Through their impact on resource availability, habitat heterogeneity and environmental filters, ecosystem engineers have a key role in the process of community assembly and dynamics (Archer et al., 2020; Baiser et al., 2013; Yeakel et al., 2020). Higher diversity, as a result of engineering impact, is likely correlated with increased stability of ecological dynamics and functions (e.g. Liu et al., 2022), however, this may not be the case for all aspects of stability (Pennekamp et al., 2018). A lot of knowledge on the diversity-stability relationship comes from studies with grassland communities, where increased species richness is linked to the maintenance of complex plant communities over time (Liang et al., 2022) and as a consequence of the stability of primary production (Craven et al., 2018). In these studies, diversity also increased ecological resilience (another measure of stability) by buffering the negative impacts of perturbations such as climate variability on species loses (Oliveira et al., 2022). Yeakel et al. (2020) used a theoretical approach to study how ecosystem engineering affects the dynamics of community assembly. The authors found that increasing the number of ecosystem engineers in their model reduced the likelihood of extinctions leading to increased network stability (i.e. a smaller number of extinctions). As the number of engineers increased, mean rates of primary extinction first increased and then declined with the likelihood of secondary extinctions (i.e. follow-on extinctions triggered by primary extinctions) systematically declining. At low engineer numbers, additional resources for consumers provided by engineering increased the vulnerability of prey leading to more primary extinctions. However, when engineers were more common, the available niche space expanded, lowering competitive overlap among consumers and suppressing both primary and secondary extinctions (Yeakel et al., 2020). Redundant engineering thus increased the temporal stability of species' niches and played an important role in promoting diversity. It has been highlighted, that species coexistence is driven by occupation of different niches rather than fitness differences between species (e.g. Buche et al., 2022). Therefore, niche space expansion appears a key mechanism by which ecosystem engineers promote diversity and prevent extinctions.

An ongoing debate about the relationship between the complexity of ecological communities and their stability (De Angelis, 1975; Hatton et al., 2024; May, 1972; McCann, 2000) points to the necessity that natural interaction networks must have some contrasting, non-random structures that allow them to persist despite their complexity (Bascompte, 2010). Several network metrics have been linked to increased stability. For example, nestedness is thought to provide robustness to extinctions in mutualistic networks, because abundant core generalist species buffer against extinctions of more specialized species (Rohr et al., 2014). In contrast to mutualistic networks, food webs appear stabilized by increased compartments or clusters (Thébault & Fontaine, 2010). These contrasting architectures may be linked to indirect interactions: negative indirect effects of apparent competition could restrict the sharing of interacting partners. To prevent cascading extinctions in food webs such negative effects need to be limited to given network nodules and can thus promote lower connectance and high modularity. In contrast, positive indirect effects in mutualistic networks should favour a more connected and nested architecture (Thébault & Fontaine, 2010). Foundation plants have been shown to trigger an increase in nestedness in mutualistic plant-pollinator networks (Losapio, Schmid, et al., 2021), thereby likely increasing network stability and the provision of pollination. In our literature review, this pattern was common as in many cases the overall number of links between species in a network and links per species clearly increased when ecosystem engineers promoted an increase in species richness. This means primary and secondary consumer species in engineered food webs have a wider range of resources, a network feature likely to increase stability through increased functional diversity and redundancy (Biggs et al., 2020). The inclusion of additional engineer species may further increase stability to engineer extinctions as crucial engineering processes are provided by more than one species. Redundancy combined with a positive effect of engineering on resource availability leads to a larger number of niches, often to higher trophic diversity and longer food chains. The response of connectance in the food webs appears to be more variable across studies. Reduced connectance in engineered habitats with higher species richness can be explained by two factors. First, many studies compare the situation of a foundation species creating a diverse habitat with simple un-engineered habitats. In these simple habitats a small number of species interact more tightly as they harbour a higher proportion of generalists, or they rely on the only few resources available. Second, there is evidence that if connectance is too high, this can destabilize communities through indirect negative interactions as explained above. Ecosystem engineering may play an important role in driving the relationship between connectance and stability. The provision of structure and niche space can increase species coexistence and change the strength of interactions between consumers and their resource (e.g. predator- prey) thereby allowing for a higher number of weaker interactions. More research is urgently needed to demonstrate if this prediction holds, particularly because some engineering species can indeed reduce diversity and resources available at the community level (e.g. Zhang et al., 2004).

Ecosystem engineers control key processes that maintain the current physical state of the environment, that is moisture, light, nutrient levels thus reducing variability in a wide range of non-trophic and consumable resources (Jones et al., 2010; Sanders et al., 2014). When external conditions like temperature or water availability vary dramatically, engineers often buffer such changes and prevent species to fall outside their fundamental niche. The loss of rabbits due to disease in the UK caused the extinctions of the *Maculinea* butterfly through a substantial change in microclimate caused by higher vegetation in grassland habitats (Thomas et al., 2009). Rabbits keep the turf low and thereby increasing soil level temperature, allowing specific *Myrmica* ant species, which are obligate hosts for the butterfly larvae, to thrive. This meant that the decline of rabbits led to increased plant vegetation, unfavourable abiotic conditions for ants and the extinction of blue butterflies. Another example of crucial engineers' impact comes from animals that control the amount of standing plant biomass, for example through grazing. They act as agents in fire regimes by reducing the amount, structure and condition of fuel available for combustion, thereby decreasing the likelihood of bush fires (Foster et al., 2020). On the contrary, species like pine bark beetles (*Dendroctonus* sp.) can promote the spread of wildfires by killing extensive patches of trees (Foster et al., 2020). These two contrasting cases exemplify the fact that the part of the physical environment being altered and controlled by the engineer is crucial to assess the effect of engineers on buffering against external forces or not.

Ecosystem engineers can have widespread impacts with whole community depending on the engineering effects of a single species. This means their invasion or loss can trigger catastrophic shifts and examples include cascading effects on species diversity and community structure following the loss of iconic ecosystem engineering species like corals or kelp (Buse et al., 2008; Chowdhury et al., 2016; Fontes et al., 2020; Hoffman et al., 2016; Rossi et al., 2013), or the extinction of prairie dogs (genus *Cynomys*; Kotliar et al., 1999). Prairie dogs that were once among the most abundant mammalian herbivores in North America have been decreasing dramatically particularly due to the exotic sylvatic plague, against which they are highly sensitive (Smith et al., 2009). The decline in prairie dogs has been followed by declines of many other species, likely due to the loss of the habitat that these mammals create through burrowing and grazing activities (Kotliar et al., 1999). Another example of such a cascading extinction comes from the semi-arid northern Negev Desert. In this ecosystem, a dramatic decline of the facilitating engineer shrub *Noaea mucronate* during very dry periods, led to significant declines in overall plant diversity at different scales (Hoffman et al., 2016). Even declines in the population size of an engineer species can lead to the loss of the engineering impact thus triggering extinctions as shown by (Säterberg et al., 2013) who reported that functional extinctions can drive diversity loss. Considering these examples, we can expect a marked impact on communities when engineering species are added or lost, for example through range expansion, invasion, or species extinction. As we discussed in the previous section, the resilience of a system will rely of the functional redundancy of key engineering processes, with "back-up" species providing a buffer against losses. This knowledge is important to understand how engineering can help or hamper adaptation to future conditions of climate change and habitat change. Engineering traits and functional redundancy in those traits provided may offer an opportunity for developing conservation strategies that address future challenges. These challenges include cascading extinctions where directly and indirectly linked species (by any type of interaction) become extinct through knock-on effects within networks (Kehoe et al., 2021).

Exotic engineer species are often associated with reduced diversity in engineered habitats as they may disrupt native community structure (Emery-Butcher et al., 2020). However, this may not be a general pattern but very much depends on the consequences of the engineering. For example, Romero et al. (2015) found no evidence for exotic engineer species having a different impact to native species in their meta-analysis. Similarly, our review suggests that species richness and network complexity can stay largely unchanged, be increased or reduced when exotic engineers arrive in a new habitat. Again, this depends on the impact by the exotic engineer either increasing or decreasing habitat heterogeneity or nutrient availability (Crooks, 2002). For example, the algae *Didymosphenia geminate* reaches large densities when settles as invasive species. This species is an engineer through the creation of dense filamentous mats and it reduced diversity because many local fauna is not capable of moving in these thick structures, thereby reducing the available habitat and resources (Ladrera et al., 2018). Native ecosystem engineers can promote invasions by exotic species (Bandano et al., 2007; Kleinhesselink et al., 2014; Wright et al., 2016) or increase resistance to invasions (Corenblit et al., 2014). Cushion plants can enable exotic plants to get established especially at higher elevations, suggesting that ecosystem engineering by native species can promote biological invasions especially in harsh environments, leading to higher abundances of invaders than those expected in the absence of engineers (Bandano et al., 2007). In contrast, Corenblit et al. (2014) found that habitat engineering by woody plants through increased elevation and sediment in riparian habitats increased the resistance of plant communities to invasion by exotic species during biogeomorphic successions. This shows that ecosystem engineering by acting on community assembly is likely to modulate the invasion of native habitats.

4 | CONCLUSIONS

Engineer species are an important driver of network structure and stability. The engineering effects can often be the backbone of an ecosystem with the loss of the engineer species causing significant changes. This is pronounced for ecosystem engineers that facilitate other habitat modifiers thereby markedly increasing habitat complexity (e.g. Angelini & Silliman, 2014; Borst et al., 2019). In this case, in a hierarchy of facilitative interactions, a basal habitat former (e.g. tree) creates living space for an intermediate habitat former (e.g. moss) that in turn creates living space for focal organisms. Such habitat cascades often enhance species abundance and diversity in ecosystems such as forests, salt marshes, seagrass meadows, and seaweed beds (Thomsen et al., 2010). A study demonstrating how invasive ants ultimately shift predation preferences in lions (Kamaru et al., 2024) further highlights how diverse and interconnected the mechanisms driving community interactions can be, being in this example a cascade of linked habitat forming, behavioural changes, and mutualistic interactions. This underlines the necessity to better understand the role of habitat modification in driving ecosystem dynamics and stability. Experimental demonstration of the relative strength of the main pathways proposed in our theoretical framework (and their effect on community stability), however, is still needed for many ecosystems (Figure 1). Yeakel et al. (2020) demonstrate how the integration of ecosystem engineering into network simulation can lead to powerful predictions about the relationship between engineering and stability. Theory and empirical evidence need to inform each other to move the research field in a direction that allows us to understand the true nature of ecological interaction networks and their response to perturbations.

Changing climates and habitats will affect the roles that engineers play in maintaining ecosystems, and this should be a priority for future research (Coggan et al., 2018). Ecosystem engineers may well be key components of communities when restoring disturbed habitats and managing conservation areas. Engineering traits such as controlling structure, sedimentation, stability of soils, temperature, moisture levels, wind speed, currents, available resources and light levels can help predicting community assembly and stability. These engineering services or disservices thus need to be considered when selecting species to protect, or to be targeted in eradication programs against invasive species. In conservation programs, for example, species that create habitat heterogeneity and novel niches that promote diversity, or the stability of ecosystem functionality should be a priority.

AUTHOR CONTRIBUTIONS

DS and EF wrote the manuscript and created the figures. DS conducted the literature search.

ACKNOWLEDGMENTS

D.S. is supported by a BBSRC Discovery Fellowship BB/X010473/1. EF is currently funded by the Agence Nationale de la Recherche (ANR) via the PRIMA S2 2018 project INTOMED and by CIRAD. We are grateful to Arjen Biere for insightful comments on an earlier version of this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data base used in this review are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.z34tmpgnw.

ORCID

Dirk Sanders https://orcid.org/0000-0003-2383-8693
Enric Frago https://orcid.org/0000-0001-8817-1303

REFERENCES

Alvarez-Filip, L., Gill, J. A., & Dulvy, N. K. (2011). Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. *Ecosphere*, *2*, art118.

Anderson, C. B., & Rosemond, A. D. (2010). Beaver invasion alters terrestrial subsidies to subantarctic stream food webs. *Hydrobiologia*, *652*, 349–361.

Angelini, C., & Silliman, B. R. (2014). Secondary foundation species as drivers of trophic and functional diversity: Evidence from a tree–epiphyte system. *Ecology*, *95*, 185–196.

Archer, S. K., Kahn, A. S., Thiess, M., Law, L., Leys, S. P., Johannessen, S. C., Layman, C. A., Burke, L., & Dunham, A. (2020). Foundation species abundance influences food web topology on glass sponge reefs. *Frontiers in Marine Science*, *799*, 549478.

Arredondo-Núñez, A., Badano, E., & Bustamante, R. (2009). How beneficial are nurse plants? A meta-analysis of the effects of cushion plants on high-Andean plant communities. *Community Ecology*, *10*, 1–6.

Baiser, B., Whitaker, N., & Ellison, A. M. (2013). Modeling foundation species in food webs. *Ecosphere*, *4*, art146.

Bandano, E. I., Villarroel, E., Bustamante, R. O., Marquet, P. A., & Cavieres, L. A. (2007). Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *Journal of Ecology*, *95*, 682–688.

Barbosa, M., Fernandes, G. W., & Morris, R. J. (2019). Interaction engineering: Non-trophic effects modify interactions in an insect galler community. *Journal of Animal Ecology*, *88*, 1168–1177.

Baruzzi, C., & Krofel, M. (2017). Friends or foes? Importance of wild ungulates as ecosystem engineers for amphibian communities. *North-Western Journal of Zoology*, *13*, 320–325.

Bascompte, J. (2010). Structure and dynamics of ecological networks. *Science*, *329*, 765–766.

Biggs, C. R., Yeager, L. A., Bolser, D. G., Bonsell, C., Dichiera, A. M., Hou, Z., Keyser, S. R., Khursigara, A. J., Lu, K., & Muth, A. F. (2020). Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. *Ecosphere*, *11*, e03184.

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

Borst, A. C. W., Angelini, C., ten Berge, A., Lamers, L., Derksen-Hooijberg, M., & van der Heide, T. (2019). Food or furniture: Separating trophic and non-trophic effects of Spanish moss to explain its high invertebrate diversity. *Ecosphere*, *10*, e02846.

Breviglieri, C. P. B., Romero, G. Q., Mega, A. C. G., & da Silva, F. R. (2019). Are cecropia trees ecosystem engineers? The effect of decomposing Cecropia leaves on arthropod communities. *Biotropica*, *51*, 562–571.

Brun, P., Zimmermann, N. E., Graham, C. H., Lavergne, S., Pellissier, L., Münkemüller, T., & Thuiller, W. (2019). The productivity-biodiversity relationship varies across diversity dimensions. *Nature Communications*, *10*, 5691.

Buche, L., Spaak, J. W., Jarillo, J., & De Laender, F. (2022). Niche differences, not fitness differences, explain predicted coexistence across ecological groups. *Journal of Ecology*, *110*, 2785–2796.

Buse, J., Ranius, T., & Assmann, T. (2008). An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. *Conservation Biology*, *22*, 329–337.

Callaway, R. M. (2007). *Positive interactions and interdependence in plant communities*. Springer.

Cheng, C., Gao, M., Zhang, Y., Long, M., Wu, Y., & Li, X. (2021). Effects of disturbance to moss biocrusts on soil nutrients, enzyme activities, and microbial communities in degraded karst landscapes in southwest China. *Soil Biology and Biochemistry*, *152*, 108065.

Chowdhury, G. W., Zieritz, A., & Aldridge, D. C. (2016). Ecosystem engineering by mussels supports biodiversity and water clarity in a heavily polluted lake in Dhaka, Bangladesh. *Freshwater Science*, *35*, 188–199.

Christianen, M. J. A., van der Heide, T., Holthuijsen, S. J., van der Reijden, K. J., Borst, A. C. W., & Olff, H. (2017). Biodiversity and food web indicators of community recovery in intertidal shellfish reefs. *Biological Conservation*, *213*, 317–324.

Coggan, N. V., Hayward, M. W., & Gibb, H. (2018). A global database and "state of the field" review of research into ecosystem engineering by land animals. *Journal of Animal Ecology*, *87*, 974–994.

Corenblit, D., Steiger, J., Tabacchi, E., González, E., & Planty-Tabacchi, A.-M. (2014). Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic connectivity. *River Research and Applications*, *30*, 45–59.

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J. A., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M., De Luca, E., Ebeling, A., Griffin, J. N., Hector, A., … Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology & Evolution*, *2*, 1579–1587.

Craven, D., van der Sande, M. T., Meyer, C., Gerstner, K., Bennett, J. M., Giling, D. P., Hines, J., Phillips, H. R. P., May, F., Bannar-Martin, K. H., Chase, J. M., & Keil, P. (2020). A cross-scale assessment of productivity–diversity relationships. *Global Ecology and Biogeography*, *29*, 1940–1955.

Crooks, J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos*, *97*, 153–166.

Davoult, D., Surget, G., Stiger-Pouvreau, V., Noisette, F., Riera, P., Stagnol, D., Androuin, T., & Poupart, N. (2017). Multiple effects of a Gracilaria vermiculophylla invasion on estuarine mudflat functioning and diversity. *Marine Environmental Research*, *131*, 227–235.

De Angelis, D. L. (1975). Stability and Connectance in food web models. *Ecology*, *56*, 238–243.

De Smet, B., Fournier, J., De Troch, M., Vincx, M., & Vanaverbeke, J. (2015). Integrating ecosystem engineering and food web ecology: Testing the effect of biogenic reefs on the food web of a soft-bottom intertidal area. *PLoS One*, *10*, e0140857.

De Smet, B., van Oevelen, D., Vincx, M., Vanaverbeke, J., & Soetaert, K. (2016). Lanice conchilega structures carbon flows in soft-bottom intertidal areas. *Marine Ecology Progress Series*, *552*, 47–60.

Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., Healy, K., Jackson, A. L., Lurgi, M., McClean, D., O'Connor, N. E., O'Gorman, E. J., & Yang, Q. (2016). Navigating the complexity of ecological stability. *Ecology Letters*, *19*, 1172–1185.

Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E., & Emmerson, M. C. (2013). On the dimensionality of ecological stability. *Ecology Letters*, *16*, 421–429.

Duarte, L., Rossi, F., Docal, C., & Viejo, R. M. (2015). Effects of alga Fucus serratus decline on benthic assemblages and trophic linkages at its retreating southern range edge. *Marine Ecology Progress Series*, *527*, 87–103.

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

Ellison, A. M., Bank, M.S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., Lovett, G. M., Mohan, J., Orwig, D. A., Rodenhouse, N. L., Sobczak, W. V., Stinson, K. A., Stone, J. K., Swan, C. M., Thompson, J., Von Holle, B., & Webster, J. R. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, *3*, 479–486.

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

Estes, J. A., & Duggins, D. O. (1995). Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs*, *65*, 75–100.

Filazzola, A., & Lortie, C. J. (2014). A systematic review and conceptual framework for the mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, *23*, 1335–1345.

Fontes, B. L., Desbiez, A. L. J., Massocato, G. F., Srbek-Araujo, A. C., Sanaiotti, T. M., Bergallo, H. G., Ferreguetti, A. C., Noia, C. H. R., Schettino, V. R., & Valls, R. (2020). The local extinction of one of the greatest terrestrial ecosystem engineers, the giant armadillo (*Priodontes maximus*), in one of its last refuges in the Atlantic Forest, will be felt by a large vertebrate community. *Global Ecology and Conservation*, *24*, e01357.

Foster, C. N., Banks, S. C., Cary, G. J., Johnson, C. N., Lindenmayer, D. B., & Valentine, L. E. (2020). Animals as agents in fire regimes. *Trends in Ecology & Evolution*, *35*, 346–356.

Franklin, J. F., Shugart, H. H., & Harmon, M. E. (1987). Tree death as an ecological process. *Bioscience*, *37*, 550–556.

Gibb, H., Silvey, C. J., Robinson, C., L'Hotellier, F. A., & Eldridge, D. J. (2021). Experimental evidence for ecological cascades following threatened mammal reintroduction. *Ecology*, *102*, e03191.

Golubkov, S., Tiunov, A., & Golubkov, M. (2021). Food-web modification in the eastern gulf of Finland after invasion of *Marenzelleria arctia* (Spionidae, Polychaeta). *NeoBiota*, *66*, 75–94.

Gómez-Aparicio, L., Zamora, R., Gómez, J. M., Hódar, J. A., Castro, J., & Baraza, E. (2004). Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, *14*, 1128–1138.

Graham, M. H. (2004). Effects of local deforestation on the diversity and structure of Southern California Giant kelp forest food webs. *Ecosystems*, *7*, 341–357.

Griffen, B. D., Riley, M. E., Cannizzo, Z. J., & Feller, I. C. (2017). Indirect effects of ecosystem engineering combine with consumer behaviour to determine the spatial distribution of herbivory. *Journal of Animal Ecology*, *86*, 1425–1433.

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S., & Wilson, W. G. (2007). Ecosystem engineering in space and time. *Ecology Letters*, *10*, 153–164.

Hatton, I. A., Mazzarisi, O., Altieri, A., & Smerlak, M. (2024). Diversity begets stability: Sublinear growth and competitive coexistence across ecosystems. *Science*, *383*, eadg8488.

Heidrich, L., Bae, S., Levick, S., Seibold, S., Weisser, W., Krzystek, P., Magdon, P., Nauss, T., Schall, P., Serebryanyk, A., Wöllauer, S., Ammer, C., Bässler, C., Doerfler, I., Fischer, M., Gossner, M. M., Heurich, M., Hothorn, T., Jung, K., … Müller, J. (2020). Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. *Nature Ecology & Evolution*, *4*, 1204–1212.

Hernández-Castellano, C., Rodrigo, A., Gómez, J. M., Stefanescu, C., Calleja, J. A., Reverté, S., & Bosch, J. (2020). A new native plant in the neighborhood: Effects on plant–pollinator networks, pollination, and plant reproductive success. *Ecology*, *101*, e03046.

Hoffman, O., de Falco, N., Yizhaq, H., & Boeken, B. (2016). Annual plant diversity decreases across scales following widespread ecosystem engineer shrub mortality. *Journal of Vegetation Science*, *27*, 578–586.

Jankowska, E., Michel, L. N., Lepoint, G., & Włodarska-Kowalczuk, M. (2019). Stabilizing effects of seagrass meadows on coastal water benthic food webs. *Journal of Experimental Marine Biology and Ecology*, *510*, 54–63.

Jankowska, E., & Włodarska-Kowalczuk, M. (2022). Habitat-builders complexity boosts associated fauna functional trait richness (*Zostera marina* meadows, Baltic Sea). *Ecological Indicators*, *144*, 109512.

Jones, A. G., Dubois, S. F., Desroy, N., & Fournier, J. (2021). Intertidal ecosystem engineer species promote benthic-pelagic coupling and diversify trophic pathways. *Marine Ecology Progress Series*, *660*, 119–139.

Jones, C. G., Gutiérrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G., & Talley, T. S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, *119*, 1862–1869.

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, *69*, 373–386.

Kamaru, D. N., Palmer, T. M., Riginos, C., Ford, A. T., Belnap, J., Chira, R. M., Githaiga, J. M., Gituku, B. C., Hays, B. R., Kavwele, C. M., Kibungei, A. K., Lamb, C. T., Maiyo, N. J., Milligan, P. D., Mutisya, S., Ng'weno, C. C., Ogutu, M., Pietrek, A. G., Wildt, B. T., & Goheen, J. R. (2024). Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey. *Science*, *383*, 433–438.

Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015). Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, *96*, 291–303.

Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A., & Berlow, E. L. (2016). How structured is the entangled Bank? The surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. *PLoS Biology*, *14*, e1002527.

Kehoe, R., Frago, E., & Sanders, D. (2021). Cascading extinctions as a hidden driver of insect decline. *Ecological Entomology*, *46*, 743–756.

Kleinhesselink, A. R., Magnoli, S. M., & Cushman, J. H. (2014). Shrubs as ecosystem engineers across an environmental gradient: Effects on species richness and exotic plant invasion. *Oecologia*, *175*, 1277–1290.

Kotliar, N. B., Baker, B. W., Whicker, A. D., & Plumb, G. (1999). A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management*, *24*, 177–192.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*, 592–599.

Kristensen, E. (2008). Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research*, *59*, 30–43.

Ladrera, R., Gomà, J., & Prat, N. (2018). Effects of Didymosphenia geminata massive growth on stream communities: Smaller organisms and simplified food web structure. *PLoS One*, *13*, e0193545.

Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, A., Jablonka, E., & Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151019.

Largaespada, C., Guichard, F., & Archambault, P. (2012). Meta-ecosystem engineering: Nutrient fluxes reveal intraspecific and interspecific feedbacks in fragmented mussel beds. *Ecology*, *93*, 324–333.

Law, A., McLean, F., & Willby, N. J. (2016). Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshwater Biology*, *61*, 486–499.

Liang, M., Baiser, B., Hallett, L. M., Hautier, Y., Jiang, L., Loreau, M., Record, S., Sokol, E. R., Zarnetske, P. L., & Wang, S. (2022). Consistent stabilizing effects of plant diversity across spatial scales and climatic gradients. *Nature Ecology & Evolution*, *6*, 1669–1675.

Liautaud, K., Barbier, M., & Loreau, M. (2020). Ecotone formation through ecological niche construction: The role of biodiversity and species interactions. *Ecography*, *43*, 714–723.

Liu, J., Matthews, T. J., Zhong, L., Liu, J., Wu, D., & Yu, M. (2020). Environmental filtering underpins the Island species—Area relationship in a subtropical anthropogenic archipelago. *Journal of Ecology*, *108*, 424–432.

Liu, S., García-Palacios, P., Tedersoo, L., Guirado, E., van der Heijden, M. G. A., Wagg, C., Chen, D., Wang, Q., Wang, J., Singh, B. K., & Delgado-Baquerizo, M. (2022). Phylotype diversity within soil fungal functional groups drives ecosystem stability. *Nature Ecology & Evolution*, *6*, 900–909.

Losapio, G., Norton Hasday, E., Espadaler, X., Germann, C., Ortiz-Sánchez, F. J., Pont, A., Sommaggio, D., & Schöb, C. (2021). Facilitation and biodiversity jointly drive mutualistic networks. *Journal of Ecology*, *109*, 2029–2037.

Losapio, G., Schmid, B., Bascompte, J., Michalet, R., Cerretti, P., Germann, C., Haenni, J.-P., Neumeyer, R., Ortiz-Sánchez, F. J., Pont, A. C., Rousse, P., Schmid, J., Sommaggio, D., & Schöb, C. (2021). An experimental approach to assessing the impact of ecosystem engineers on biodiversity and ecosystem functions. *Ecology*, *102*, e03243.

May, R. M. (1972). Will a large complex system be stable? *Nature*, *238*, 413–414.

McCann, K. S. (2000). The diversity–stability debate. *Nature*, *405*, 228–233.

Miyashita, T., & Takada, M. (2007). Habitat provisioning for aboveground predators decreases detritivores. *Ecology*, *88*, 2803–2809.

Montoya, J. M., Pimm, S. L., & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, *442*, 259–264.

Moore, J. W. (2006). Animal ecosystem engineers in streams. *Bioscience*, *56*, 237–246.

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

Nauta, J., Christianen, M. J. A., Temmink, R. J. M., Fivash, G. S., Marin-Diaz, B., Reijers, V. C., Didderen, K., Penning, E., Borst, A. C. W., Heusinkveld, J. H. T., Zwarts, M., Cruijsen, P. M. J. M., Hijner, N., Lengkeek, W., Lamers, L. P. M., van der Heide, T., Bouma, T. J., van der Wal, D., Olff, H., & Govers, L. L. (2023). Biodegradable artificial reefs enhance food web complexity and biodiversity in an intertidal soft-sediment ecosystem. *Journal of Applied Ecology*, *60*, 541–552.

Nummi, P., Arzel, C., & Sauramo, V. (2021). Populations in stable and variable habitats: Green and common sandpiper in a beaver-influenced landscape. *Global Ecology and Conservation*, *28*, e01678.

Nummi, P., Kattainen, S., Ulander, P., & Hahtola, A. (2011). Bats benefit from beavers: A facilitative link between aquatic and terrestrial food webs. *Biodiversity and Conservation*, *20*, 851–859.

Nummi, P., & Pöysä, H. (1997). Population and community level responses in Anas-species to patch disturbance caused by an ecosystem engineer, the beaver. *Ecography*, *20*, 580–584.

Olff, H., Alonso, D., Berg, M. P., Eriksson, B. K., Loreau, M., Piersma, T., & Rooney, N. (2009). Parallel ecological networks in ecosystems. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *364*, 1755–1779.

Oliveira, B. F., Moore, F. C., & Dong, X. (2022). Biodiversity mediates ecosystem sensitivity to climate variability. *Communications Biology*, *5*, 628.

Orwin, K. H., Wardle, D. A., Towns, D. R., St. John, M. G., Bellingham, P. J., Jones, C., Fitzgerald, B. M., Parrish, R. G., & Lyver, P. O. B. (2016). Burrowing seabird effects on invertebrate communities in soil and litter are dominated by ecosystem engineering rather than nutrient addition. *Oecologia*, *180*, 217–230.

Osunkoya, O. O., & Perrett, C. (2011). *Lantana camara* L. (Verbenaceae) invasion effects on soil physicochemical properties. *Biology and Fertility of Soils*, *47*, 349–355.

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., Fronhofer, E. A., Ganesanandamoorthy, P., Garnier, A., Griffiths, J. I., Greene, S., Horgan, K., Massie, T. M., Mächler, E., Palamara, G. M., Seymour, M., & Petchey, O. L. (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, *563*, 109–112.

Pereira, C. C., Sperandei, V.d. F., Henriques, N. R., Silva, Á. A. N., Fernandes, G. W., & Cornelissen, T. (2021). Gallers as leaf rollers: Ecosystem engineering in a tropical system and its effects on arthropod biodiversity. *Ecological Entomology*, *46*, 470–481.

Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature Ecology & Evolution*, *1*, 0101.

Prugh, L. R., & Brashares, J. S. (2012). Partitioning the effects of an ecosystem engineer: Kangaroo rats control community structure via multiple pathways. *Journal of Animal Ecology*, *81*, 667–678.

Rogers-Bennett, L., & Catton, C. A. (2019). Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Scientific Reports*, *9*, 15050.

Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic systems. *Science*, *345*, 1253497.

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

Rooney, N., McCann, K., Gellner, G., & Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, *442*, 265–269.

Rossi, F., Gribsholt, B., Gazeau, F., Di Santo, V., & Middelburg, J. J. (2013). Complex effects of ecosystem engineer loss on benthic ecosystem response to detrital macroalgae. *PLoS One*, *8*, e66650.

Samways, M. J., McGeoch, M. A., & New, T. R. (2010). *Insect conservation: A handbook of approaches and methods*. Oxford University Press.

Sanders, D., Jones, C. G., Thébault, E., Bouma, T. J., van der Heide, T., van Belzen, J., & Barot, S. (2014). Integrating ecosystem engineering and food webs. *Oikos*, *123*, 513–524.

Sanders, D., & van Veen, F. J. F. (2011). Ecosystem engineering and predation: The multi-trophic impact of two ant species. *Journal of Animal Ecology*, *80*, 569–576.

Säterberg, T., Sellman, S., & Ebenman, B. (2013). High frequency of functional extinctions in ecological networks. *Nature*, *499*, 468–470.

Schlatter, D. C., Baugher, C. M., Kahl, K., Huggins, D. R., Johnson-Maynard, J. L., & Paulitz, T. C. (2019). Bacterial communities of soil and earthworm casts of native Palouse Prairie remnants and no-till wheat cropping systems. *Soil Biology and Biochemistry*, *139*, 107625.

Siple, M. C., & Donahue, M. J. (2013). Invasive mangrove removal and recovery: Food web effects across a chronosequence. *Journal of Experimental Marine Biology and Ecology*, *448*, 128–135.

Smith, J. G., Tomoleoni, J., Staedler, M., Lyon, S., Fujii, J., & Tinker, M. T. (2021). Behavioral responses across a mosaic of ecosystem states restructure a sea otter–urchin trophic cascade. *Proceedings of the*

National Academy of Sciences of the United States of America, *118*, e2012493118.
Smith, K. F., Behrens, M. D., & Sax, D. F. (2009). Local scale effects of disease on biodiversity. *EcoHealth*, *6*, 287–295.
St. John, M. G., Bellingham, P. J., Walker, L. R., Orwin, K. H., Bonner, K. I., Dickie, I. A., Morse, C. W., Yeates, G. W., & Wardle, D. A. (2012). Loss of a dominant nitrogen-fixing shrub in primary succession: Consequences for plant and below-ground communities. *Journal of Ecology*, *100*, 1074–1084.
Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*, 866–880.
Stringer, A. P., & Gaywood, M. J. (2016). The impacts of beavers Castor spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. *Mammal Review*, *46*, 270–283.
Tegner, M., & Dayton, P. (2000). Ecosystem effects of fishing in kelp forest communities. *ICES Journal of Marine Science*, *57*, 579–589.
Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, *329*, 853–856.
Thomas, J. A., Simcox, D., & Clarke, R. T. (2009). Successful conservation of a threatened Maculinea butterfly. *Science*, *325*, 80–83.
Thomsen, M. S., Wernberg, T., Altieri, A., Tuya, F., Gulbransen, D., McGlathery, K. J., Holmer, M., & Silliman, B. R. (2010). Habitat cascades: The conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integrative and Comparative Biology*, *50*, 158–175.
Tuma, J., Eggleton, P., & Fayle, T. M. (2020). Ant-termite interactions: An important but under-explored ecological linkage. *Biological Reviews*, *95*, 555–572.
van der Zee, E. M., Angelini, C., Govers, L. L., Christianen, M. J., Altieri, A. H., van der Reijden, K. J., Silliman, B. R., van de Koppel, J., van der Geest, M., & van Gils, J. A. (2016). How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20152326.
Washko, S., Roper, B., & Atwood, T. B. (2020). Beavers alter stream macroinvertebrate communities in north-eastern Utah. *Freshwater Biology*, *65*, 579–591.
Wetzel, W. C., Screen, R. M., Li, I., McKenzie, J., Phillips, K. A., Cruz, M., Zhang, W., Greene, A., Lee, E., & Singh, N. (2016). Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. *Ecology*, *97*, 427–438.
Wilson, S. D., & Peltzer, D. A. (2021). Per-gram competitive effects and contrasting soil resource effects in grasses and woody plants. *Journal of Ecology*, *109*, 74–84.
Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, *132*, 96–101.
Wright, J. T., Gribben, P. E., & Latzel, S. (2016). Native ecosystem engineer facilitates recruitment of invasive crab and native invertebrates. *Biological Invasions*, *18*, 3163–3173.
Wyckhuys, K. A. G., Graziosi, I., Burra, D. D., & Walter, A. J. (2017). Phytoplasma infection of a tropical root crop triggers bottom-up cascades by favoring generalist over specialist herbivores. *PLoS One*, *12*, e0182766.
Xu, Q., Yang, X., Song, J., Ru, J., Xia, J., Wang, S., Wan, S., & Jiang, L. (2022). Nitrogen enrichment alters multiple dimensions of grassland functional stability via changing compositional stability. *Ecology Letters*, *25*, 2713–2725.
Yeakel, J. D., Pires, M. M., de Aguiar, M. A. M., O'Donnell, J. L., Guimarães, P. R., Gravel, D., & Gross, T. (2020). Diverse interactions and ecosystem engineering can stabilize community assembly. *Nature Communications*, *11*, 3307.
Zhang, Y., Richardson, J. S., & Negishi, J. N. (2004). Detritus processing, ecosystem engineering and benthic diversity: A test of predator-omnivore interference. *Journal of Animal Ecology*, *73*, 756–766.
Zhong, Z., Li, G., Sanders, D., Wang, D., Holt, R. D., & Zhang, Z. (2022). A rodent herbivore reduces its predation risk through ecosystem engineering. *Current Biology*, *32*, 1869–1874.e1864.
Zhong, Z., Li, X., Sanders, D., Liu, Y., Wang, L., Ortega, Y. K., Pearson, D. E., & Wang, D. (2021). Soil engineering by ants facilitates plant compensation for large herbivore removal of aboveground biomass. *Ecology*, *102*, e03312.

SUPPORTING INFORMATION

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

Appendix S1. Literature search.

How to cite this article: Sanders, D., & Frago, E. (2024). Ecosystem engineers shape ecological network structure and stability: A framework and literature review. *Functional Ecology*, *00*, 1–14. https://doi.org/10.1111/1365-2435.14608