iScience

CellPress
REVIEWS

Review

Foundation Species, Non-trophic Interactions, and the Value of Being Common

Aaron M. Ellison[1,*]

Foundation species define ecosystems, control the biological diversity of associated species, modulate critical ecosystem processes, and often have important cultural values and resonance. This review summarizes current understanding of the characteristics and traits of foundation species and how to distinguish them from other "important" species in ecological systems (e.g., keystone, dominant, and core species); illustrates how analysis of the structure and function of ecological networks can be improved and enriched by explicit incorporation of foundation species and their non-trophic interactions; discusses the importance of pro-active identification and management of foundation species as a cost-effective and efficient method of sustaining valuable ecosystem processes and services and securing populations of associated rare, threatened, or endangered species; and suggests broader engagement of citizen-scientists and non-specialists in the identification and study of foundation species and their biological and cultural values.

INTRODUCTION

Foundation species determine local and regional biodiversity, control ecosystem dynamics, and have intrinsic value to the people who live with or near them. Originally identified in deep-water benthic marine environments (Dayton, 1972), foundation species now are recognized to occur in a wide range of terrestrial, aquatic, and marine systems worldwide (Bruno and Bertness, 2001; Ellison et al., 2005; Thomsen et al., 2010; Angelini et al., 2011; Bulleri et al., 2016). Interactions between foundation species and others associated with them generally are non-trophic (i.e., are different from the trophic, or "who-eats-whom" interactions of food webs). These non-trophic interactions usually are neglected in ecological networks unless they are lumped within compartments representing other primary producers or basal resources (Baiser et al., 2013; van der Zee et al., 2016; Borst et al., 2018). Furthermore, foundation species are common and abundant and have received less attention from regulatory agencies and environmental professionals who are focused on conservation and management of rare, threatened, or endangered species (Gaston and Fuller, 2007, 2008). Yet without foundation species, populations of species targeted for conservation and management may not be sustainable, and the ecosystems processes on which they, and we, depend may be sorely compromised.

In this review, I first distinguish foundation species from other "important" types of species in ecological systems. I then illustrate how analysis of the structure and function of ecological networks can be improved and enriched via the explicit incorporation of foundation species and their non-trophic effects. One of the key challenges for research on the effects of foundation species is reliably identifying them. Because non-trophic effects usually are more subtle and harder to detect than trophic or competitive interactions, it can take many years—often decades—to acquire sufficient data to distinguish foundation species from non-foundation species. I discuss how the combination of new statistical methods and use of traditional ecological or cultural knowledge may help to accelerate the time to reliable identification of foundation species. More rapid identification of foundation species also can define new priorities and methods for conservation and management of individual species and entire ecosystems. Such prioritization can simultaneously and cost-effectively support conservation and protection of other, often rare, species. Throughout this review, I highlight targets for new research directions focused on foundation species, their system-wide effects, and their conservation and management.

WHAT ARE FOUNDATION SPECIES?

Characteristics of Foundation Species

Ecologists identify foundation species based on three defining characteristics (Ellison et al., 2005). First, they are numerically abundant and account for most of the biomass in an ecosystem. Second, they are at or near the base of the directional interaction networks that characterize ecosystems (e.g., sponges or

[1]Harvard Forest, Harvard University, Petersham, MA 01366, USA

*Correspondence: aellison@fas.harvard.edu

https://doi.org/10.1016/j.isci.2019.02.020

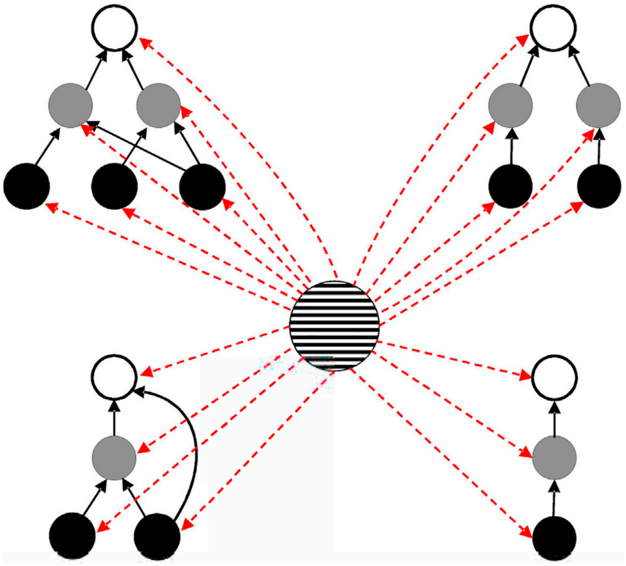

Figure 1. The Central, Non-trophic Place of a Foundation Species in an Ecological Network

A foundation species (center, striped) is the most abundant species in an ecological network. It primarily interacts non-trophically (dashed red arrows) with both basal and consumer species of several sub-webs in ways that directly affect feeding interactions (solid black arrows) among other species (e.g., refuge from predation) or other non-feeding interactions (e.g., metabolism, reproduction). These sub-webs are illustrated as simplified food-web diagrams in which white nodes (circles) represent apex predators (i.e., species that themselves have no predators), gray nodes represent intermediate consumers (i.e., species that are both predators of species at lower trophic levels and prey of the apex predators), and black nodes are basal species that otherwise have no prey (e.g., most plants). Illustration by Benjamin Baiser.

corals in the marine benthos, trees in forests; Figures 1 and 2A). Third, their abundant connections to other species in an ecological network mostly reflect non-trophic or mutualistic interactions, including providing structural support for other species, significantly altering ecosystem properties to [dis]favor other species, altering metabolic rates of associated species, and modulating fluxes of energy and nutrient flow through the system (Baiser et al., 2013; Figure 2).

Thus, foundation species are likely to be connected—directly and indirectly—to many more species than any other species in ecological networks. More broadly, we perceive foundation species differently from other species: foundation species define a system and are inseparable from it. Examples of the latter include redwood trees (*Sequoia sempervirens*) in "redwood forests," mangroves (especially *Rhizophora* species) in "mangrove forests," and hermatypic (reef-forming) corals (e.g., *Acropora*, *Montastrea*, or *Porites* species) of "coral reefs" (Ellison et al., 2005). These examples also illustrate that foundation species may be a single species, such as redwoods or eastern hemlock (*Tsuga canadensis*) trees, functionally similar species within a genus (*Montastrea* spp. on coral reefs), or unrelated species united by convergent traits (e.g., mangroves; see also Bittleston et al., 2016). In the latter case, when two or more foundation species of similar growth forms co-occur, the combination of specificity and complementarity of their foundational effects can non-redundantly promote associated species diversity and ecosystem processes (e.g., Angelini et al., 2011; Hupp et al., 2017; Mora et al., 2018).

Foundation Species Are Different from Other Ecologically Important Species

George Orwell, whose reduction of the Seven Commandments of Animalism to the maxim "[A]ll animals are equal, but some animals are more equal than others" (Orwell, 1945: 112), could be considered the conceptual parent of the foundation species concept. But the marine ecologist Paul Dayton was the first scientist to articulate that foundation species are those species that "have roles in the maintenance of the community disproportionate to the abundance or biomass of the species" (Dayton, 1972: 84). Dayton (1972) posited that species occupying different trophic levels could be considered foundation species in the environmentally stable benthos of McMurdo Sound. His initial candidates were the three abundant

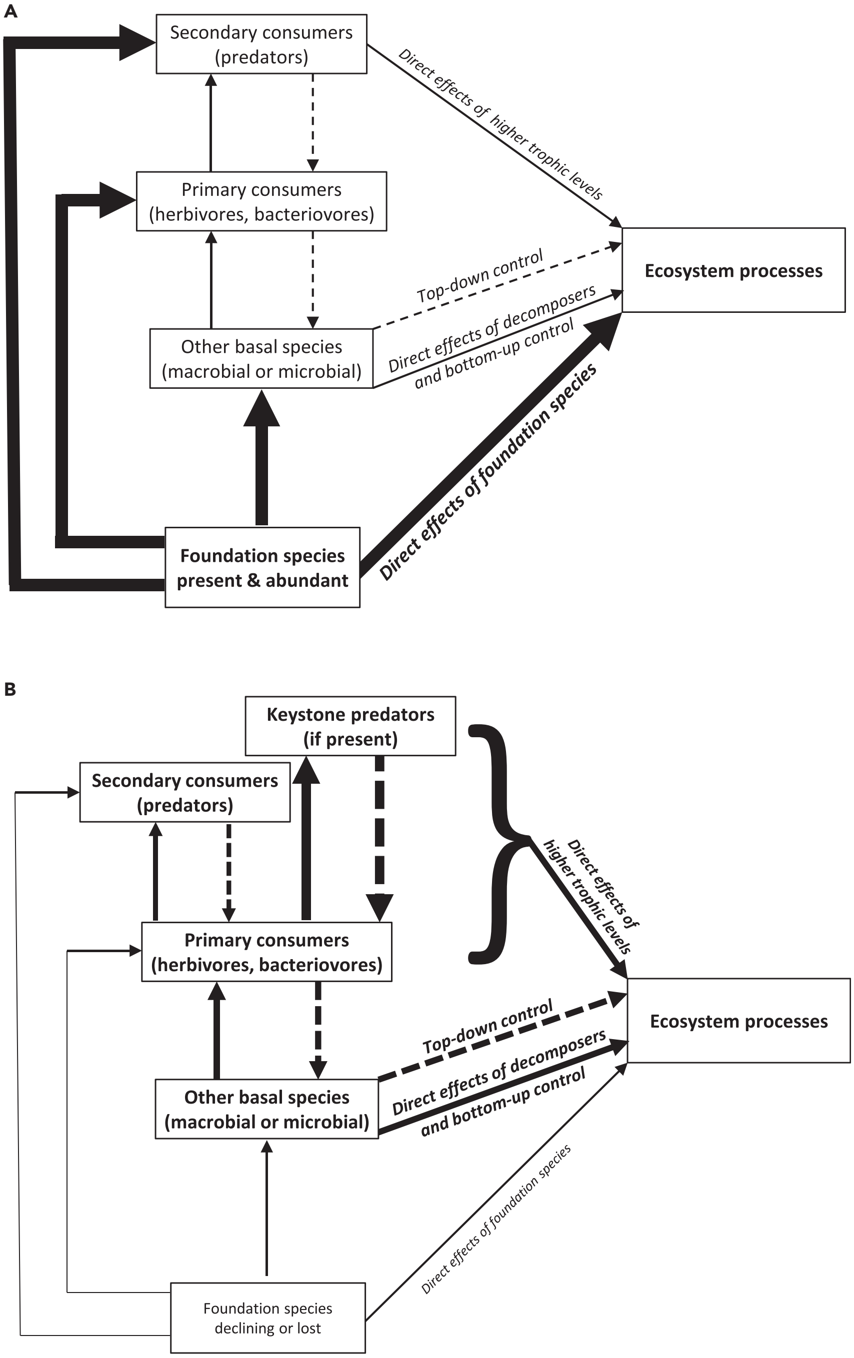

Figure 2. Direct and Indirect Effects of Foundation Species on Biodiversity and Ecosystem Processes

Conceptual model for disentangling the direct effects (solid lines) of foundation species on species diversity (richness or abundance-weighted richness) and ecosystem processes from indirect effects (dashed lines) of species associated with foundation species.

(A) When a foundation species is present and abundant, it is the dominant controller on both the composition and abundance of associated species and on core ecosystem processes (strength of influence indicated by width of arrows).

(B) When the foundation species declines or is lost from the system, bottom-up processes such as microbial control of decomposition drive ecosystem processes, whereas top-down controllers such as keystone predators or herbivores have large effects on species diversity of primary consumers and basal species. Elaborated from the conceptual model of Ellison (2010).

"glass" sponges (Lyssacinosida: Rossellidae) species and the comparatively rare demosponge *Mycale acerata* (Poecilosclerida: Mycalidae) that together formed the structural matrix of the benthic assemblage, and three of their predatory starfish (Asteroidea: Valvatida) that fed on the sponges and regulated their population densities. At the same time, he noted that at least one of the starfish, *Odontaster validus*, was a keystone predator (sensu Paine, 1966) in the system. Keystone predators (including keystone herbivores sensu Poelman and Kessler, 2016) are not foundation species, however. Unlike foundation species, keystone predators are generally uncommon and their mode of action is through trophic effects (Valls et al., 2015), not the non-trophic ones of foundation species (Figures 1 and 2).

Dayton (1972) did provide examples of foundation species from terrestrial and freshwater ecosystems, but ecologists working in those habitats appear to have been unaware of his work. In subsequent decades, researchers working in terrestrial ecosystems independently suggested many different types of ecologically "important" species that had some or all the attributes of foundation species (Box 1). These include *core species* (Hanski, 1982), *dominant species* (Grime, 1987), *extended keystone species* (Holling, 1992; but see Valls et al., 2015), *structural species* (Huston, 1994), *ecosystem engineers* (Jones et al., 1994), and *cornerstone species* (Bracken and Low, 2012). Still others have suggested a hierarchy of foundation species: "primary" foundation species such as those described earlier may host secondary (tertiary, etc.) foundation species that provide additional structure at smaller spatial and temporal scales (e.g., Dickson and Whitham, 1996; Altieri et al., 2007; Thomsen et al., 2010, 2016; 2018; Angelini et al., 2011; Keith et al., 2017).

As virtually all species modify their environment to some degree (*niche construction* sensu Odling-Smee et al., 2003), contemporary ecologists follow Dayton (1972) in distinguishing foundation species (*sensu stricto*) from other species that modify their local environment because the activities of foundation species are disproportionate to their abundance or biomass. Although foundation species most frequently are common and abundant, Bracken and Low (2012) suggested that uncommon or rare *cornerstone species* also could exert strong "bottom-up" effects on higher trophic levels (similar to Dayton's characterization of *Mycale acerata*). Their rarity disqualifies cornerstone species from also being foundation species; by analogy, the cornerstone of a building does not support it in the same way as its massive foundation.

A Formal Definition of Foundation Species

Based on nearly 50 years of research, a foundation species can be defined as a species (or group of functionally similar taxa) that dominates an assemblage numerically and in overall size (usually mass), determines the diversity of associated taxa through non-trophic interactions, and modulates fluxes of nutrients and energy at multiple control points in the ecosystem it defines.

FOUNDATION SPECIES IN WEBS OF ECOLOGICAL INTERACTIONS

The different roles that foundation species play in the ecosystems they define can be illustrated most clearly by visualizing their connections within ecological networks (Figures 1 and 2) and the consequences of their loss (Figure 3). Like any general network, an ecological network includes a set of interacting nodes (e.g., species, pools of nutrients, habitat patches) connected by edges (or links) that represent relationships between nodes. Ecologists historically focused most of their attention on two types of relationships: trophic interactions and flows of nutrients and energy (often independent of species identity); recent additions include bipartite networks of plants and their pollinators (e.g., Olesen et al., 2007) and movement of individuals (or entire assemblages) among habitat patches (i.e., metapopulations [Hanski, 1999] or metacommunities [Liebold and Chase, 2017]).

One of the most important influences on community and ecosystem ecology of considering the structuring roles of foundation species and other autogenic ecosystem engineers has been the increasing recognition of the commonness and magnitude of non-trophic facilitative and mutualistic interactions (e.g., Bertness and Callaway, 1994; Bruno et al., 2003; Callaway, 2007; Bascompte and Jordano, 2013; Filazzola and Lortie, 2014). In many of these cases, foundation species ameliorate abiotic stressors and play fundamental roles in promoting species coexistence (Figure 3, Table 1). The loss of foundation species from non-trophic plant-plant interaction networks may lead to cascading extinctions of associated species (Table 1; Verdu and Valiente-Banuet, 2008; Losapio and Schöb, 2017).

The more recent application of general network theories to systems of interacting species has led to rapid advancement in understanding the processes and dynamics of ecological systems (Lau et al., 2017). Such

Box 1. The Different Kinds of Important Species

Dayton (1972: 86) defined foundation species as being "disproportionately important to the continued maintenance of the existent community structure." Six years earlier, marine ecologists had identified one other type of "important" species, the keystone predator (Paine, 1966). Although marine ecologists consistently have differentiated foundation species from keystone species (Valls et al., 2015), there has been a proliferation of terms used for other "important" species in terrestrial and freshwater ecosystems. These include (updated from Ellison et al., 2005):

- *Core species* are locally abundant and regionally common; they are associated with satellite species that are sparse or rare (sensu Rabinowitz, 1981). An associated metapopulation model (the *core-satellite hypothesis*) predicts relationships between a species' local abundance and its regional distribution (Hanski, 1982, 1999). Core species have some of the biodiversity-controlling properties of foundation species, but their effects on ecosystem processes such as fluxes of energy and nutrients were not specified.
- *Dominant species* are plants that competitively exclude subordinate species by garnering most of the available resources (nutrients) and contributing most to primary productivity (Grime, 1987). Dominant species have effects like foundation tree species on local species richness (Ellison et al., 2019), but the former do not have the facilitative effects on biodiversity of the latter.
- *Keystone herbivores or predators* increase local species richness by preferentially feeding on dominant competitors and creating physical space where subordinate competitors can persist. Keystone predators were initially identified and defined for marine invertebrates in rocky intertidal habitats (Paine, 1966). Keystone herbivores modify the local relative abundance of plants or the animals (mostly insects) that feed on them by (1) preferentially grazing on dominant competitors and opening up physical space for subordinate species (i.e., in the same way as a keystone predator) or (2) inducing phenotypic changes in plant physical, structural, or chemical defenses (Hunter, 1992; Poelman and Kessler, 2016). Unlike foundation species, keystone herbivores and predators rarely are common.
- *Extended keystone species* control and organize terrestrial ecosystems (Holling, 1992). Although appealing in principle, it has proven difficult to distinguish an extended keystone species from any other "important" species.
- *Structural species or habitat formers* create physical structures, produce variability in physical conditions, provide resources, and create habitat for associated ("interstitial") species (Huston, 1994; Thomsen et al., 2010). Like core species, structural and habitat-forming species can be thought of as playing the biodiversity-controlling role of foundation species, but their effects on ecosystem processes remain unspecified.
- *Ecosystem engineers* cause physical state changes in biotic or abiotic materials and modulate energy and nutrient fluxes to other species in their ecosystem (Jones et al., 1994). Jones et al. (1994) distinguished "allogenic" from "autogenic" ecosystem engineers. Allogenic engineers transform living or nonliving materials from a raw state to an engineered state. In contrast, the engineered products of an autogenic engineer are the living or dead tissues of the engineer itself. In both cases, the engineered products either modulate the flow of resources (e.g., energy, nutrients) to other species or alter the dynamics of an environmental variable (e.g., frequency or intensity of precipitation, water flow, or fire) that in turn modulates resource flows. The Class 5 autogenic ecosystem engineers of Jones et al. (1994) are the closest analog to Dayton's (1972) foundation species. However, foundation species may directly provide autogenic resources (such as tree-holes or other support structures) to associated species, whereas this type of direct effect is excluded from the definition of an ecosystem engineer by Jones et al. (1994).
- *Cornerstone species* are rare, basal species (e.g., algae, sessile invertebrates) that can affect local richness and relative abundance of species at higher trophic levels (Bracken and Low, 2012). As with many foundation species, the effects of cornerstone species are primarily facilitative: they provide food or habitat for mobile grazers and predators that have keystone-like effects on species diversity. However, cornerstone species are rare and their ecosystem-level effects have not yet been explored.
- *Benefactor species* provide some positive benefit to other ("beneficiary") species. The positive role of a benefactor species usually depends on context: its effects are positive (mutualistic) in stressful environments or habitats but may be negative (competitive) in more benign environments or habitats (Bulleri et al., 2018).
- *Climate rescuers* are structural species or habitat formers whose resistance or resilience to ongoing climatic change may ameliorate local environmental conditions to a degree that associated species can survive in otherwise inhospitable conditions (Bulleri et al., 2018). The resistance or resilience to climatic change of taxa identified as foundation species is an open area of research.

"systems thinking" has a long history in ecology, ranging from Darwin's entangled bank (Darwin, 1859) through the quantification of trophic dynamics (e.g., Lindeman, 1942) and the definition of "cybernetic ecosystems" (Patten, 1959) to contemporary formalizations of "network ecology" (e.g., Borrett et al., 2014;

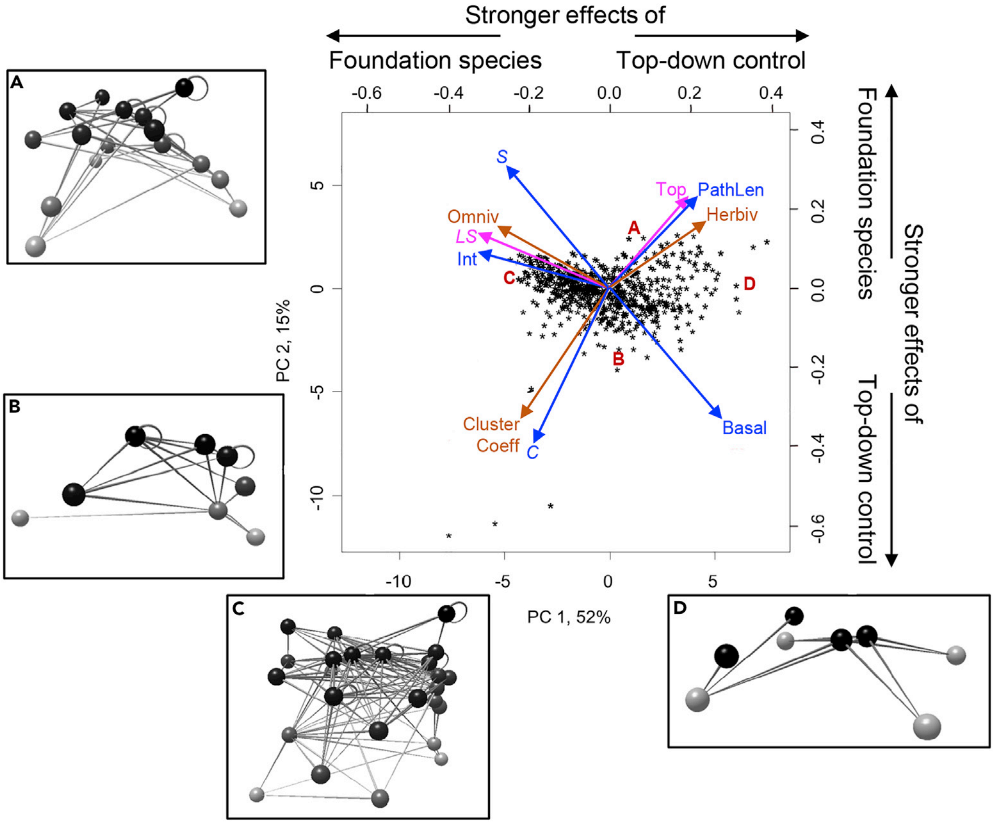

Figure 3. Simulated Effects of Foundation Species on the Structure of Ecological Networks

Simulated food webs that either included foundation species (as in Figure 2A) that have non-trophic control of associated basal species and higher trophic levels (dashed red arrows in Figure 1) and trophic interactions among associated species (solid black arrows in Figure 1) or lacked foundation species (as in Figure 2B) and have predominantly trophic control of species interactions. The inset network diagrams are representative food webs when non-trophic foundation species effects (A and C) or predator-based trophic effects (B and D) predominated. Individual data points are the scores in principal component space (the first two axes explain 67% of the total variance in the data) summarizing food-web metrics for the 100 different simulations; the location in principal component space of each of the lettered insets is indicated with the corresponding letter on the plot. The simulations were initialized with a network structure with or without non-trophic effects modified from the niche model of Williams and Martinez (2000) and predator-prey biomass ratios = 100. Dynamics of each interaction web used an allometric predator-prey model (Brose et al., 2006). Each model food web was initialized with $S = 30$ species, a connectance value $C = 0.15$, foundation species effects (if present) on associated species described by a general metabolic saturating function (Brown et al., 2004; Otto and Day, 2007), and initially uniform distributions (on the interval [0.5, 1.0]) of biomass assigned to individual species. Simulations ran for 2000 time-steps, after which we computed ten standard metrics of food-web structure for each web (abbreviations and direction of influence in principal component space in matching colors; see Table 1 for explanations and principal component loadings of food-web metrics). Figure modified from Basier et al. (2013; CC-BY) with additional annotations on the top and right axes.

Poisot et al., 2016). But the increasing awareness of the importance of ecological interaction networks has taken on more immediacy as Earth confronts an anthropogenically caused "sixth mass extinction" (Leakey and Lewin, 1996). Conservation biologists are now thinking beyond extinctions of individual species to consider the causes, cascading consequences, and management of the extinction of ecological interactions (e.g., Valiente-Banuet et al., 2015).

As noted earlier, the most important roles in an ecosystem of a foundation species are unrelated to its being either a consumer or a resource (e.g., Kendrick et al., 2015; Case et al., 2017; Bulleri et al., 2018; Record et al., 2018; Figures 2 and 3). Non-trophic interactions including facilitation and amelioration of stressful abiotic conditions (Bertness and Callaway, 1994; Callaway, 2007; Bulleri et al., 2018), parasitism (Dobson and Hudson, 1986), and competition (Schoener, 1983) all contribute to the structure and organization of ecological communities, but their integration into studies and analyses of ecological networks is sporadic.

Metric[a]	Initial Food-Web (t = 2,000)		After Foundation Species Removal (t = 4,000)	
	PC-1	PC-2	PC-1	PC-2
S	−0.34	0.40	0.36	0.39
LS	−0.40	0.17	0.45	−0.02
C	−0.22	−0.46	0.16	−0.66
Top	0.26	0.32	−0.23	−0.06
Int	−0.40	0.11	0.41	0.15
Basal	0.32	−0.38	−0.39	−0.15
Herbiv	0.28	0.20	−0.17	0.06
Omniv	−0.36	0.19	0.34	0.00
PathLen	0.26	0.31	−0.18	0.59
ClusterCoeff	−0.27	−0.41	0.30	−0.14

Table 1. Principal Component Loadings for Ten Metrics of Food-Web Structure after Initialization and Food-Web Assembly to Approximate Equilibrium (t = 2,000 Modeled Time-Steps) and after the Foundation Species Was Removed (t = 4,000 Time-Steps)

[a] Food-web metrics are: *S*, number of species; *LS*, the linkage density (L/S, where L is the number of observed edges in the network diagram [links between species]); *C*, connectance (L/S^2); Top, percentage of top predators (taxa that have no other predators); Int, percentage of intermediate taxa (those with both predators and prey); Basal, percentage of primary producers (taxa without prey); Herbiv, percentage of herbivores (taxa that feed on only basal species); Omniv, percentage of omnivores (taxa that feed on multiple trophic levels); PathLen, the characteristic path length (the mean shortest set of undirected links between pairs of species); ClusterCoeff, the clustering coefficient (the probability that two taxa linked to the same taxon are also linked). See Baiser et al. (2013) and Lau et al. (2017) for additional details.

For example, Kéfi et al. (2012) considered three categories of non-trophic interactions that vary in their influence on other species. The first are interactions that directly modify feeding parameters (e.g., consumption rate); examples include coastal habitat formers such as bivalves (clams or mussels) or mangroves (e.g., Thomsen et al., 2016; Bulleri et al., 2018) and those in forests such as nurse logs (e.g., Hofgaard, 1993) or hunting perches for predators created by tree branches. The second modify non-feeding parameters, including metabolism and reproduction (Baiser et al., 2013). The third modify imports and exports of nutrients, energy, or materials across ecosystem boundaries; examples include dispersal of seeds out of a patch or transfers of biomass (nutrients, energy) from aquatic to terrestrial systems (e.g., Helfield and Naiman, 2006; Ignace et al., 2018). Foundation species can affect all of these, and other, non-trophic interactions in ecological networks, and their effects are expected to be disproportionate to their already high abundance (Baiser et al., 2013; Figure 3, Table 1). These species not only support the networks of interacting species that feed on each other and that interact in ways that do not involve eating or being eaten, but also are network hubs (Ma and Ellison, 2019) that connect many subsidiary networks (Figures 1 and 3).

THE IMPORTANCE OF CONTEXT AND THE VALUE OF LONG-TERM DATA

There are many hundreds of studies of the roles that important species play in a wide variety of ecosystems (e.g., Petraitis and Dudgeon, 2005; Proffitt et al., 2005; Schiel, 2006; Altieri et al., 2007; Olyarnik and Stachowicz, 2012; Peters and Yao, 2012; Bishop et al., 2013; Ellison, 2014; Angelini et al., 2015; Ellison and Degrassi, 2017; Elumeeva et al., 2017; Keith et al., 2017; Derksen-Hooijberg et al., 2018; Haggerty et al., 2018; O'Brien and Scheibling, 2018; Record et al., 2018; Ruocco et al., 2018). However, deciding whether an ''important'' species plays foundational roles (disproportionate to its abundance or biomass) requires framing its foundational role as a hypothesis, not an assertion (Ellison, 2014).

The broader context is critical in identifying foundation species (Angelini et al., 2011). A species (or group of species) that plays a foundational role in one system at a certain place or at a certain time may not play a foundational role elsewhere. This has been explored in detail for foundation species in forests, where long-term observational data combined with reconstructions from tree-rings of climate and changing assembles of species have suggested that a species' foundational role can unfold at different successional stages (Lutz and Halpern, 2006; Halpern and Lutz, 2013; Ellison et al., 2014, 2019; Freund et al., 2015) or in response to different degrees of disturbance (Uriarte et al., 2004).

Clarifying the context and teasing apart, identifying, and characterizing even a small fraction of the many interactions that foundation species control usually requires long-term observations and manipulative experiments done with an eye toward testing the hypothesis that a particular species is a foundation species. The aforementioned studies on the emergence of foundational roles that species play in forests all took decades of observations and experiments (see also Kane et al., 2011; Keith et al., 2011; Wyse et al., 2014). Similar long-term observations and experiments with long-lived coastal and marine foundation species (Altieri and van de Koppel, 2013), such as salt-marsh grasses (e.g., Sala et al., 2008) and seagrasses (e.g., Hughes et al., 2009), have revealed clear support for foundational roles of specific species in specific contexts. Further such studies in a broad array of systems should be a priority for future research (Ellison and Degrassi, 2017).

CONSERVATION VALUE OF FOUNDATION SPECIES

Because foundation species create habitats for other species, modulate ecosystem processes, and in many ways shape our perception of the world around us, we should be paying much more attention to identifying and protecting them while they are common, rather than waiting until their populations decline below functional levels (Gaston and Fuller, 2007; 2008; Frimpong, 2018). Yet because they are usually common, foundation species themselves rarely have been of conservation concern until they are threatened and already declining. This is unfortunate, because the myriad interactions controlled by foundation species are difficult to recover after they have declined in abundance or disappear entirely from the ecosystem that they otherwise define.

Mathematical modeling illustrates that when foundation species decline or disappear, the interaction networks that depend on them will be simplified as individual species that depend on the foundation species are lost (Baiser et al., 2013; Valiente-Banuet et al., 2015; Losapio and Schöb, 2017; Kardol et al., 2018; Figure 3). Some of these associated species disappear because they have strong, direct interactions with the foundation species (e.g., Cavieres and Badano, 2009; Barringer et al., 2012; Tomback et al., 2016), whereas others disappear because of indirect effects—they depend on species that themselves depend on the foundation species (Cáceres et al., 2015).

Many of the species that depend on foundation (or other dominant) species are uncommon or rare; they may be of conservation or management concern or formally listed as threatened or endangered by state, national, or international organizations (e.g., Berg et al., 1994; Martikainen et al., 2000; Bruno et al., 2003; Stauffer et al., 2004; Hughes et al., 2009). The decline or loss of a foundation species can reduce overall ecosystem functionality at an even faster rate than the loss of individual species or their pairwise interactions (Baiser et al., 2013; Valiente-Banuet et al., 2015; Tomback et al., 2016). In a positive feedback loop, further decline of foundation species can be accelerated by trophic release of other mid-level herbivores or predators that switch to feeding on increasingly rare foundation species (Clements and Hay, 2018). If foundation species are replaced by one or more species that do not control ecosystem functions to the same extent, the entire system may be rearranged (Bulleri et al., 2018; Figure 3). New interaction networks will be established, but none will be as well linked as in the system supported by a foundation species (Bertness et al., 2015). Conversely, when a foundation species is introduced outside its native range, its effects on associated species can be reversed. An illustrative example is the positive effects that *Prosopis* shrubs have on species diversity in its native range in South America become negative in its introduced range in India and Hawai'i (Kaur et al., 2012).

Scientific rationales, such as data-driven demonstrations of the importance of foundation species, have failed to encourage their conservation while they are still common or the maintenance of their commonness. Maintaining a species as common is different from preserving its occurrence (representation) in an ecosystem or across the landscape. These different goals may be conflated: contrast the *goal* of the US Geological Survey's National Gap Analysis Project of identifying conservation gaps that help keep common species common with its *objective* (designed to implement this goal) of mapping predicted distributions of terrestrial vertebrate species and documenting their representativeness in land-cover types (USGS, 2016). Other reasons are needed to protect common foundation species. These could include using the value of rarity to conserve the rarity of commonness itself, the value of diversity, or the importance of a sense of place.

The Value of Rarity

Perhaps unsurprisingly, we tend to think about, care for, and manage rare species much more than common ones, even though the functional value of rare species (and other rare things) is rarely in line with their scientific importance in an ecosystem (Metrick and Weitzman, 1996, Koford and Tschoegl, 1998, Gerber, 2016; but see Bracken and Low, 2012 and Jain et al., 2014 for counter-examples). Even among rare species, most resources directed at implementing recovery plans for their populations or protecting necessary "habitat" (which may include a foundation species) for their continued persistence are showered on only a handful of taxa (Metrick and Weitzman, 1996; Gerber, 2016).

Ecological systems consist of a mixture of rare and common species, and the general shape of the frequency distribution of abundance of individual species is that of a "reverse-J": a few very abundant species and many with low abundance (Fisher et al., 1943; Preston, 1948; MacArthur, 1960; Ulrich et al., 2010; Figure 4). If rarity alone confers value (Koford and Tschoegl, 1998), then the rarity of commonness should be valued (Gaston and Fuller, 2007, 2008) and common species—especially those with clearly important ecosystem functions—should be worth preserving in their common state. Gerber (2016) and others have argued that conservation "triage" should be used to better allocate resources from rare and endangered species that are receiving most conservation funding but are still declining to other rare and endangered species that are currently underfunded but have better odds for recovery (Cornwall, 2018). In contrast, I would argue that an even better "return" on conservation investment could come from pro-active protection, conservation, and management of common foundation species that create and maintain the habitats on which so many other species depend.

The Value of Diversity

Diversity—measured as the number of species (often weighted by their abundance) in a locality ("alpha diversity") or a region ("gamma diversity"), or the quotient of the two ("beta diversity") (Ellison, 2010)—generally confers greater ecosystem functionality (e.g., Loreau et al., 2001; Tilman et al., 2014; Mori et al., 2018; Schuldt et al., 2018; but see Pillai and Gouhier, 2019). Diversity also is valued by many people as an attribute in its own right (Solomon, 2006). Foundation species can confer diversity by creating habitat for other species (Huston, 1994; Bulleri et al., 2018) or by lending "patchiness" to a landscape, thus increasing its beta diversity (Orwig et al., 2013; Ellison et al., 2016, 2019; Record et al., 2018). This can occur not only at the landscape level (Ellison et al., 2019) but also at very small scales when two co-occurring foundation species have complementary effects (e.g., Hupp et al., 2017). But foundation species do more than simply add another species or functional group into a mixture. Rather, foundation species knit together the ecosystems they create into heterogeneous (sensu Kolumbus et al., 2016), interacting complex systems. The role of diversity, heterogeneity, and species complementarity in maintaining complex adaptive systems is fundamentally different from standard assessments of the relationship between diversity (as simply the numbers of species) and ecosystem functionality (most commonly net primary production) (e.g., Loreau et al., 2001; Tilman et al., 2014; Pillai and Gouhier, 2019) and remains much less understood (Page, 2010; Losapio and Schöb, 2017).

A Sense of Place

Foundation species define the systems they create and maintain. In some cases, they increase associated biodiversity, in other cases they reduce it (Ellison et al., 2019). In some cases, they increase system-wide productivity, in other cases they suppress it (Foster, 2014). But in all cases, they provide us with a sense of place and a touchstone to which we often return. For example, the poet Robert Frost (1923) wrote about eastern hemlock (*Tsuga canadensis*), a foundation tree species in eastern North America, in *Dust of Snow*. In the first stanza of her poem *Florida*, Elizabeth Bishop (1946) observes that the eponymous state (United States) is held together by "mangrave" roots (the Oxford English Dictionary [OED, 2018a] synonymizes "mangrave" with mangrove, although one could argue that it refers to the "white man's grave": lands like those in what is now the United States that were subject to Western colonialism or missionary activities [OED, 2018b]), and the only ecosystem mentioned in Olu Oguibe's searing poem, *I am bound to this land by blood* (Oguibe, 2013), is a mangrove swamp. Mangrove forests fringing coral islands like Key West

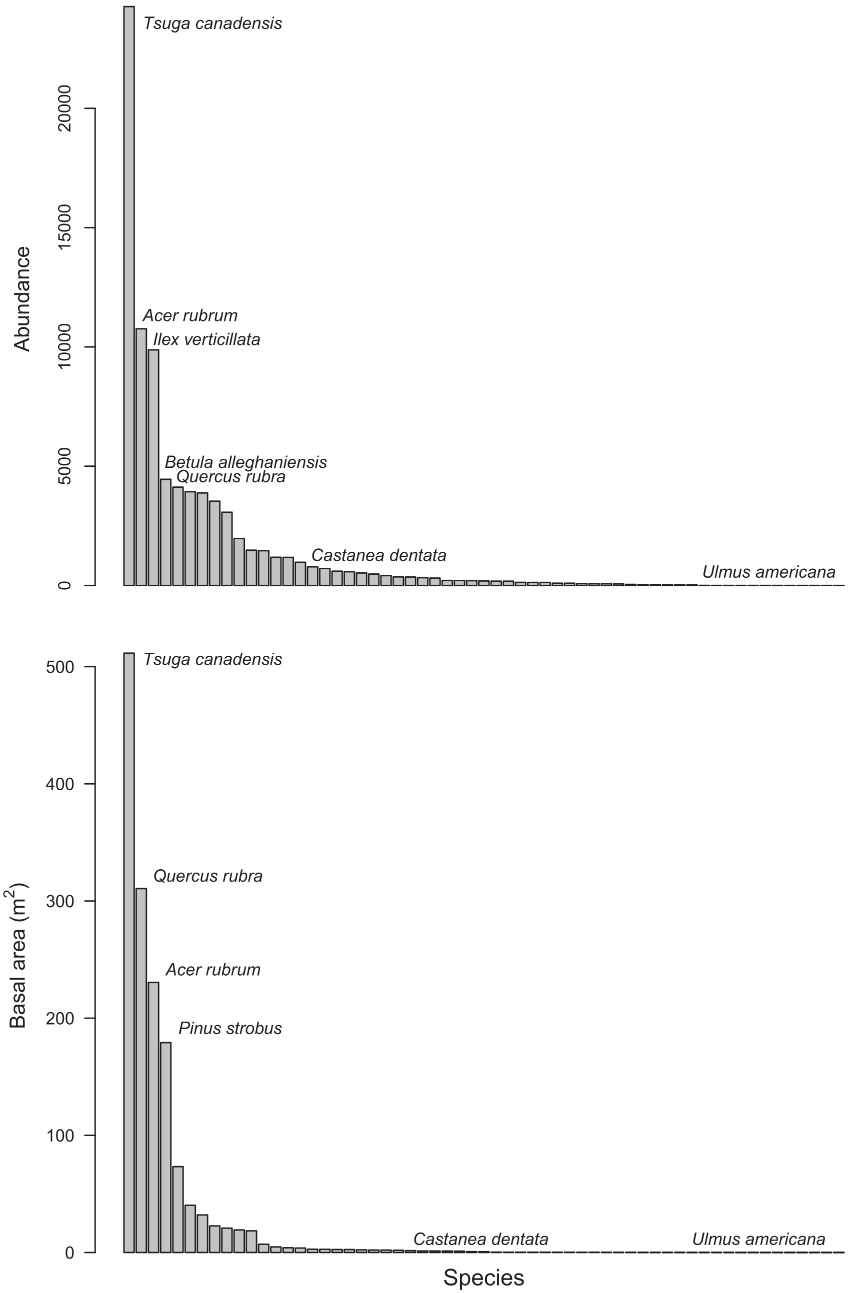

Figure 4. The Rarity of Commonness

Species-abundance distributions of the 51 species of living woody plants in the 35-ha forest dynamics plot at Harvard Forest illustrate the rarity of being common. In this plot, all 83,813 trees and shrubs with stems >1 cm in diameter were tagged, mapped, and measured. Abundance is represented in two ways: number of stems (top panel) and total basal area (m^2) covered by each species (bottom panel) in the plot. In both cases, the foundation species in this forest (*Tsuga canadensis*; Ellison, 2014) is the most abundant (both numerically and in size). The two species of widespread conservation and management concern, American chestnut (*Castanea dentata*) and American elm (*Ulmus americana*), are in the long tail of rare species in this plot, as they would be in any mixed deciduous forest in the eastern United States. Data from Orwig et al. (2015).

where Bishop wrote *Florida*, along the rivers near Oguibe's homeland of Aba, Nigeria, and elsewhere in the world are formed and organized by foundation species trees in the genus *Rhizophora* (Schutte and Byers, 2017).

Because foundation species are widely recognized by non-specialists and provide a sense of place, it may be easy to generate widespread support for their protection and conservation. On the other hand, familiarity with rare taxa of known conservation concern has been shown to lead to the erroneous perception that these taxa are not threatened (Courchamp et al., 2018), so care is needed in motivating both conservation concern and appropriate financial resources for the protection of foundation species.

PRO-ACTIVE IDENTIFICATION OF FOUNDATION SPECIES

Ecological research aimed at understanding the role of foundation species and the preservation, conservation, and management of them depends on accurately distinguishing foundation species from other important ones. Although every species has value and studying the natural history and ecology of a species in the field confers importance on it, it is critical to test the hypothesis that a species of interest is a foundation species, not simply to assert it (Ellison, 2014). Such testing is a difficult, lengthy process (e.g., Sala et al., 2008; Hughes et al., 2009; Kane et al., 2011; Keith et al., 2011; Altieri and van de Koppel, 2013; Ellison, 2014; Wyse et al., 2014).

Although ecologists often recognize the role of foundation species while they are still common, the importance of conserving or managing them rarely has been articulated until they are declining or disappearing (e.g., Ellison et al., 2005; Byers et al., 2006; Gedan et al., 2011; Wyse et al., 2014; Tomback et al., 2016; Clements and Hay, 2018). More rapid identification of foundation species could help basic researchers focus attention on key individual, population, or ecosystem-level attributes for in-depth study and analysis while motivating applied researchers and conservation professionals to direct resources to protecting foundation species before they decline. Pro-active identification of foundation species is being approached in at least two ways.

Statistics and Data Mining

The increasing availability of large observational and experimental datasets on species co-occurrences, species-environment relationships, and the multiple roles that individual species and associated biodiversity play in maintaining a variety of ecosystem processes (e.g., Green and Short, 2003; Short et al., 2007; Fischer et al., 2010; Spalding et al., 2010; Anderson-Teixeira et al., 2015; Manning et al., 2018; ReefBase, 2018) present an opportunity to statistically sieve large numbers of species in search of candidates for further analysis as potential foundation species. For example, knowing that eastern hemlock (*Tsuga canadensis*) is a foundation species in eastern North American forest (Ellison, 2014), we have used codispersion analysis (Cuevas et al., 2013) to explore pairwise species co-occurrences (Buckley et al., 2016a), relationships between species occurrences and underlying environmental gradients (Buckley et al., 2016b), and temporal changes in spatial patterns of species abundances (Case et al., 2016, 2017) to identify two statistical "fingerprints" of a foundation species in hemlock-dominated and other forests (Ellison et al., 2019). These fingerprints are (1) foundation species are statistical outliers from the expected "reverse-J" size-frequency and abundance-diameter distributions and (2) foundation tree species have negative effects on alpha diversity of associated woody plants and positive effects on their beta diversity at most spatial lags and directions (Ellison et al., 2019). This method has yet to be applied to ecosystems other than forests, and comparative efforts would be illuminating, especially in systems where foundation species and their facilitative effects ameliorate abiotic stresses (Bertness and Callaway, 1994). Similarly, the simulation models by Baiser et al. (2013) suggest that quantitative relationships among metrics of food-web structures can indicate the presence or absence of a foundation species (Figure 3, Table 1).

Traditional Ecological Knowledge and Citizen-Science

Because foundation species characteristically define the systems they create, nonspecialists and citizen-scientists should be engaged in identifying and articulating the cultural value of foundation species and other ecologically important ones (e.g., Ens et al., 2015; Costanza et al., 2017). Numerous studies have found that members of traditional cultures and other nonspecialists can identify individual species, their functional values, and ecosystem characteristics that are well correlated with ecological indicator species and quantitative metrics used by ecologists to assess ecosystem states (e.g., Zhao et al., 2016; Charnley et al., 2017; Done et al., 2017; Lyver et al., 2018). People from all backgrounds and with a wide range of abilities now have access to tools for identifying species and contributing to growing databases on species occurrences and traits (Farnsworth et al., 2013). Individual and cultural memories also may add substantial historical insights about ecological changes that are otherwise unavailable (Lyver et al., 2018). Synthesizing all these information streams with available scientific data could lead to more rapid progress in identifying candidate foundation species. Finally, because traditional ecological knowledge does not separate people from "nature" (Berkes et al., 1998), its inclusion also may help engender broader and deeper support for the conservation and management of foundation species and the ecosystems that depend on them (e.g., Ens et al., 2015; Charnley et al., 2017; Poe et al., 2014). Such rapid identification and protection of foundation species may yet help to staunch the accelerating tide of the global decline of biodiversity.

ACKNOWLEDGMENTS

The evolution of my thinking about the ecology, conservation, and management of foundation species has benefitted from many years of discussion with my students, post-docs, and colleagues at the Harvard Forest, with particular shout-outs to Ben Baiser, Hannah Buckley, Brad Case, Ally Degrassi, and Diana Tomback. I thank Nick Gotelli for suggesting the layout of the graphical abstract and David Buckley Borden for producing it. My work on foundation species has been supported by the Harvard Forest and by several grants from the US National Science Foundation: DBI 04-52254, 10-03938, and 14-59519, and DEB 06-20443 and 12-37491. This is a contribution from the Harvard Forest Long-Term Ecological Research (LTER) program.

AUTHOR CONTRIBUTIONS

A.M.E. wrote the paper.

REFERENCES

Altieri, A.H., and van de Koppel, J. (2013). Foundation species in marine ecosystems. In Marine Community Ecology and Conservation, M.D. Bertness, J.F. Bruno, B.R. Silliman, and J.J. Stachowicz, eds. (Sinauer Associates), pp. 37–56.

Altieri, A.H., Silliman, B.R., and Bertness, M.D. (2007). Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. Am. Nat. *169*, 195–206.

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A., Baltzer, J.L., et al. (2015). CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Glob. Change Biol. *21*, 528–549.

Angelini, C., Altieri, A.H., Silliman, B.R., and Bertness, M.D. (2011). Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience *61*, 782–789.

Angelini, C., van der Heide, T., Griffin, J.N., Morton, J.P., Derksen-Hooijberg, M., Lamers, L.P.M., Smolders, A.J.P., and Silliman, B.R. (2015). Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proc. Biol. Sci. *282*, https://doi.org/10.1098/rspb.2015.0421.

Baiser, B., Whitaker, N., and Ellison, A.M. (2013). Modeling foundation species in food webs. Ecosphere *4*, 146.

Barringer, L.E., Tomback, D.F., Wunder, M.B., and McKinney, S.T. (2012). Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark's nutcracker. PLoS One *7*, e37663.

Bascompte, J., and Jordano, P. (2013). Mutualistic Networks (Princeton University Press).

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., and Weslien, J. (1994). Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Cons. Biol. *8*, 718–731.

Berkes, F., Kislalioglu, M., Folke, C., and Gadgil, M. (1998). Exploring the basic ecological unit: ecosystem-like concepts in traditional societies. Ecosystems *1*, 409–415.

Bertness, M.D., and Callaway, R.M. (1994). Positive interactions in communities. Trends Ecol. Evol. *9*, 191–193.

Bertness, M.D., Brisson, C.P., and Crotty, S.M. (2015). Indirect human impacts turn off reciprocal feedbacks and decrease ecosystem resilience. Oecologia *178*, 231–237.

Bishop, E. (1946). North and South (Houghton Mifflin Co.).

Bishop, M.J., Fraser, J., and Gribben, P.E. (2013). Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves. Ecology *94*, 1927–1936.

Bittleston, L.S., Pierce, N.E., Ellison, A.M., and Pringle, A. (2016). Convergence in multispecies interactions. Trends Ecol. Evol. *31*, 269–280.

Borrett, S.R., Moody, J., and Edelmann, A. (2014). The rise of network ecology: maps of the topic diversity and scientific collaboration. Ecol. Modell. *200*, 371–383.

Borst, A.C.W., Verberk, W.C.E.P., Angelini, C., Schotanus, J., Wolters, J.W., Christianen, M.J.A., van der Zee, E.M., Derksen-Hooijberg, M., and van der Heide, T. (2018). Foundation species enhance food web complexity through non-trophic facilitation. PLoS One *13*, e0199152.

Bracken, M.E.S., and Low, N.H.N. (2012). Realistic losses of rare species disproportionately impact higher trophic levels. Ecol. Lett. *15*, 461–467.

Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F., et al. (2006). Consumer-resource body-size relationships in natural food webs. Ecology *87*, 2411–2417.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. (2004). Toward a metabolic theory of ecology. Ecology *85*, 1771–1789.

Bruno, J.F., and Bertness, M.D. (2001). Habitat modification and facilitation in benthic marine communities. In Marine Community Ecology, M.D. Bertness, S.D. Gaines, and M.E. Hay, eds. (Sinauer Associates), pp. 201–218.

Bruno, J.F., Stachowicz, J.J., and Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. Trends Ecol. Evol. *18*, 119–125.

Buckley, H.L., Case, B.S., and Ellison, A.M. (2016a). Using codispersion analysis to characterize spatial patterns in species co-occurrences. Ecology *97*, 32–39.

Buckley, H.L., Case, B.S., Zimmermann, J., Thompson, J., Myers, J.A., and Ellison, A.M. (2016b). Using codispersion analysis to quantify and understand spatial patterns in species-environment relationships. New Phytol. *211*, 735–749.

Bulleri, F., Bruno, J.F., Silliman, B.R., and Stachowicz, J.J. (2016). Facilitation and the niche: implications for coexistence range shifts and ecosystem functioning. Funct. Ecol. *30*, 70–78.

Bulleri, F., Eriksson, B.K., Queirós, A., Airoldi, L., Arenas, F., Arvanitidis, C., Bouma, T.J., Crowe, T.P., Davoult, D., Guizien, K., et al. (2018). Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. PLoS Biol. *16*, e2006852.

Byers, J.E., Cuddington, K., Jones, C.G., Talley, T.S., Hastings, A., Lambrinos, J.G., Crooks, J.A., and Wilson, W.G. (2006). Using ecosystem engineers to restore ecological systems. Trends Ecol. Evol. *21*, 493–500.

Cáceres, Y., Llambí, L.D., and Rada, F. (2015). Shrubs as foundation species in a high tropical alpine ecosystem: a multi-scale analysis of plant spatial interactions. Plant Ecol. Div. *8*, 147–161.

Callaway, R.M. (2007). Positive Interactions and Interdependence in Plant Communities (Springer).

Case, B.S., Buckley, H.L., Barker Plotkin, A., and Ellison, A.M. (2016). Using codispersion analysis to quantify temporal changes in the spatial pattern of forest stand structure. Chil. J. Stat. *7*, 3–15.

Case, B.S., Buckley, H.L., Barker Plotkin, A.A., Orwig, D.A., and Ellison, A.M. (2017). When a foundation crumbles: forecasting forest community dynamics associated with the decline of the foundation species. Ecosphere *8*, e01893.

Cavieres, L.A., and Badano, E.I. (2009). Do facilitative interactions increase species richness at the entire community level? J. Ecol. *97*, 1181–1191.

Charnley, S., Carothers, C., Satterfield, T., Levine, A., Poe, M.R., Norman, K., Donatuto, J., Breslow, S.J., Mascia, M.B., Levin, P.S., et al. (2017). Evaluating the best available social science or natural resource management decision-making. Environ. Sci. Policy *73*, 80–88.

Clements, C.S., and Hay, M.E. (2018). Overlooked coral predators suppress foundation species as reefs degrade. Ecology *28*, 1673–1682.

Cornwall, W. (2018). Should it be saved? Science *361*, 962–965.

Costanza, K.K.L., Livingston, W.H., Kashian, D.M., Slesak, R.A., Tardif, J.C., Dech, J.P., Diamond, A.K., Daigle, J.J., Ranco, D.J., Neptune, J.S., et al. (2017). The precarious state of a cultural keystone species: tribal and biological assessments of the role and future of black ash. J. Forest. *115*, 435–456.

Courchamp, F., Jaric, I., Albert, C., Meinard, Y., Ripple, W.J., and Chapron, G. (2018). The paradoxical extinction of the most charismatic animals. PLoS Biol. *16*, e2003997.

Cuevas, F., Porcu, E., and Vallejos, R. (2013). Study of spatial relationships between two sets off variables: a nonparametric approach. J. Nonparametr. Stat. *25*, 695–714.

Darwin, C. (1859). On the Origin of Species (John Murray).

Dayton, P.K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In Proceedings of the Colloquium on Conservation Problems in Antarctica, B.C. Parker, ed. (Allen Press), pp. 81–96.

Derksen-Hooijberg, M., Angelini, C., Lamers, L.P.M., Borst, A., Smolders, A., Hoogveld, J.R.H., de Paoli, H., van de Koppel, J., Silliman, B.R., and van der Heide, T. (2018). Mutualistic interactions amplify saltmarsh restoration success. J. Appl. Ecol. *55*, 405–414.

Dickson, L.L., and Whitham, T.W. (1996). Genetically-based plant resistance traits affect arthropods, fungi, and birds. Oecologia *106*, 400–406.

Dobson, A.P., and Hudson, P.J. (1986). Parasites, disease and the structure of ecological communities. Trends Ecol. Evol. *1*, 11–15.

Done, T., Roelfsema, C., Harvey, A., Schuller, L., Hill, J., Schläppy, M.-L., Lea, A., Bauer-Civiello, A., and Loder, J. (2017). Reliability and utility of citizen science reef monitoring data collected by Reef Check Australia, 2002–2015. Mar. Poll. Bull. *117*, 148–155.

Ellison, A.M. (2010). Partitioning diversity. Ecology *91*, 1962–1963.

Ellison, A.M. (2014). Experiments are revealing a foundation species: a case study of eastern hemlock (*Tsuga canadensis*). Adv. Ecol. *204*, 11.

Ellison, A.M., and Degrassi, A.L. (2017). All species are important, but some species are more important than others. J. Veg. Sci. *28*, 669–671.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, D.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., et al. (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. *9*, 479–486.

Ellison, A.M., Lavine, M., Kerson, P.B., Barker Plotkin, A.A., and Orwig, D.A. (2014). Building a foundation: land-use history and dendrochronology reveal temporal dynamics of a *Tsuga canadensis* (Pinaceae) forest. Rhodora *116*, 377–427.

Ellison, A.M., Barker Plotkin, A.A., and Khalid, S. (2016). Foundation species loss and biodiversity of the herbaceous layer in New England forests. Forests *7*, 9.

Ellison, A.M., Buckley, H.L., Case, B.S., Cardenas, D., Duque, Á.J., Lutz, J.A., Myers, J.A., Orwig, D.A., and Zimmerman, J.K. (2019). Species diversity associated with foundation species in temperate and tropical forests. Forests *10*, 128.

Elumeeva, T.G., Onipchenko, V.G., and Weger, M.J.A. (2017). No other species can replace them: evidence for the key role of dominants in an alpine *Festuca varia* grassland. J. Veg. Sci. *28*, 674–683.

Ens, E.J., Pert, P., Clarke, P.A., Budden, M., Clubb, L., Doran, B., Douras, C., Gaikwad, J., Gott, B., Leonard, S., et al. (2015). Indigenous biocultural knowledge in ecosystem science and management: review and insight from Australia. Biol. Conserv. *181*, 133–149.

Farnsworth, E.J., Chu, M., Kress, W.J., Neill, A.K., Best, J.H., Stevenson, R.D., Courtney, G.W., Vandyk, J.K., and Ellison, A.M. (2013). Next-generation field guides. BioScience *63*, 891–899.

Filazzola, A., and Lortie, C.J. (2014). A systematic review and conceptual framework for the mechanistic pathways of nurse plants. Glob. Ecol. Biogeogr. *23*, 1335–1345.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., et al. (2010). Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. Basic Appl. Ecol. *11*, 473–485.

Fisher, R.A., Corbet, A.S., and Williams, C.B. (1943). The relation between the number of species and the number of individuals in a random sample from an animal population. J. Anim. Ecol. *12*, 42–58.

Foster, D.R. (2014). Lament. In Hemlock: A Forest Giant on the Edge, D.R. Foster, ed. (Yale University Press), pp. 224–239.

Freund, J.A., Franklin, J.F., and Lutz, J.A. (2015). Structure of early old-growth douglas-fir forests in the Pacific Northwest. Forest Ecol. Manage. *335*, 11–25.

Frimpong, E.A. (2018). A case for conserving common species. PLoS Biol. *16*, e2004261.

Frost, R. (1923). New Hampshire: A Poem, with Notes and Grace Notes (Henry Holt & Co.).

Gaston, K.J., and Fuller, R.A. (2007). Biodiversity and extinction: losing the common and the widespread. Prog. Phys. Geogr. *31*, 213–225.

Gaston, K.J., and Fuller, R.A. (2008). Commonness, population depletion and conservation biology. Trends Ecol. Evol. *23*, 14–19.

Gedan, K.B., Altieri, A.H., and Bertness, M.D. (2011). Uncertain future of New England salt marshes. Mar. Ecol. Prog. Ser. *434*, 229–237.

Gerber, L.R. (2016). Conservation triage or injurious neglect in endangered species recovery. Proc. Nat. Acad. Sci. U S A *113*, 3563–3566.

Green, E.P., and Short, F.T. (2003). World Atlas of Seagrasses (University of California Press).

Grime, J.P. (1987). Dominant and subordinate components of plant communities: implications for succession, stability and diversity. In Colonization, Succession and Stability, A.J. Gray, M.J. Crawley, and P.J. Edwards, eds. (Blackwell Scientific Publications), pp. 413–428.

Haggerty, M.B., Anderson, T.W., and Long, J.D. (2018). Fish predators reduce kelp frond loss via a trait-mediated trophic cascade. Ecology *99*, 1574–1583.

Halpern, C.B., and Lutz, J.A. (2013). Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions. Ecol. Monogr. *83*, 221–237.

Hanski, I. (1982). Dynamics of regional distribution: the core and satellite species hypothesis. Oikos *38*, 210–221.

Hanski, I. (1999). Metapopulation Ecology (Oxford University Press).

Helfield, J.M., and Naiman, R.J. (2006). Keystone interactions: salmon and bear in riparian forests of Alaska. Ecosystems *9*, 167–180.

Hofgaard, A. (1993). Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. J. Veg. Sci. *4*, 601–608.

Holling, C.S. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol. Monogr. *62*, 447–502.

Hughes, A.R., Williams, S.L., Duarte, C.M., Heck, K.L., and Waycott, M. (2009). Associations of concern: declining seagrasses and threatened dependent species. Front. Ecol. Environ. *7*, 242–246.

Hunter, M.D. (1992). Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept. In Effects of Resource Distribution on Animal-Plant Interactions, M.D. Hunter, ed. (Academic Press), pp. 287–325.

Hupp, N., Llambí, L.D., Ramírez, L., and Callaway, R. (2017). Alpine cushion plants have species-specific effects on microhabitats and community structure in the tropical Andes. J. Veg. Sci. *28*, 928–938.

Huston, M.A. (1994). Biological Diversity: The Coexistence of Species on Changing Landscapes (Cambridge University Press).

Ignace, D.D., Fassler, A., and Bellemare, J. (2018). Decline of a foundation tree species due to invasive insects will trigger net release of soil organic carbon. Ecosphere *9*, e02391.

Jain, J., Flynn, D.E.B., Prager, C.M., Hart, G.M., DeVan, C.M., Ahrestani, F.S., Palmer, M.I., Bunker, D.E., Knops, J.M.H., Jouseau, C.F., and Naeem, S. (2014). The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. Ecol. Evol. *4*, 104–112.

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

Kane, J.M., Meinhardt, K.A., Chang, T., Cardall, B.L., Michalet, R., and Whitham, T.G. (2011). Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. Plant Ecol. *212*, 733–741.

Kardol, P., Fanin, N., and Wardle, D.A. (2018). Long-term effects of species loss on community properties across contrasting ecosystems. Nature *557*, 710–713.

Kaur, J., Gonzáles, W.L., Llambí, L.D., Soriano, P., Callaway, R., Rout, M.E., Gallaher, T.J., and Inderjit. (2012). Community impacts of *Prosopis juliflora* invasion: biogeographic and congeneric comparisons. PLoS One *7*, e44966.

Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C., and Brose, U. (2012). More than a meal…integrating non-feeding interactions into food webs. Ecol. Lett. *15*, 291–300.

Keith, A.R., Bailey, J.K., and Witham, T.G. (2011). A genetic basis to community repeatability and stability. Ecology *91*, 3398–3406.

Keith, A.R., Bailey, J.K., Lau, M.K., and Whitham, T.G. (2017). Genetics-based interactions of foundation species affect community diversity, stability and network structure. Proc. R. Soc. B *284*, 20162703.

Kendrick, J.A., Ribbons, R.R., Classen, A.T., and Ellison, A.M. (2015). Changes in canopy structure and ant assemblages affect soil ecosystem variables as a foundation species declines. Ecosphere *6*, 77.

Koford, K., and Tschoegl, A.E. (1998). The market value of rarity. J. Econ. Behav. Organ. *34*, 445–457.

Kolumbus, A., Shavit, A., and Ellison, A.M. (2016). Two roads diverge in a wood: indifference to the difference between ‘diversity’ and ‘heterogeneity’ should be resisted on epistemic and moral grounds. PhilSci Archive. http://philsci-archive.pitt.edu/id/eprint/12432.

Lau, M.K., Borrett, S.R., Baiser, B., Gotelli, N.J., and Ellison, A.M. (2017). Ecological network metrics: opportunities for synthesis. Ecosphere *8*, e01900.

Leakey, R., and Lewin, R. (1996). The Sixth Extinction: Patterns of Life and the Future of Humankind (Anchor).

Liebold, M.A., and Chase, J.M. (2017). Metacommunity Ecology (Princeton University Press).

Lindeman, R.L. (1942). The trophic-dynamic aspect of ecology. Ecology *23*, 399–418.

Loreau, M., Naeem, S.L., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., et al. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. Science *294*, 804–808.

Losapio, G., and Schöb, C. (2017). Resistance of plant-plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. Funct. Ecol. *31*, 1145–1152.

Lutz, J.A., and Halpern, C.B. (2006). Tree mortality during early forest development: a long-term study of rates, causes, and consequences. Ecol. Monogr. *76*, 257–275.

Lyver, P.O., Richardson, S.J., Gormley, A.M., Timute, P., Jones, C.J., and Tahi, B.L. (2018). Complementarity of indigenous and western scientific approaches for monitoring forest state. Ecol. Appl. *28*, 1909–1923.

Ma, S., and Ellison, A.M. (2019). Dominance network analysis provides a new framework for studying the diversity-stability relationship. Ecol. Monogr. *89*, e01358.

MacArthur, R. (1960). On the relative abundance of species. Am. Nat. *94*, 25–36.

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F.T., Mace, G., Whittingham, M.J., and Fischer, M. (2018). Redefining ecosystem multifunctionality. Nat. Ecol. Evol. *2*, 427–436.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., and Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol. Conserv. *94*, 199–209.

Metrick, A., and Weitzman, M.L. (1996). Patterns of behavior in endangered species preservation. Land Econ. *72*, 1–16.

Mora, M.A., Llambí, L.D., and Ramírez, L. (2018). Giant stem rosettes have strong facilitation effects on alpine plant communities of the tropical Andes. Plant Ecol. Div.. https://www.tandfonline.com/doi/full/10.1080/17550874.2018.1507055

Mori, A.S., Isbell, F., and Seidl, R. (2018). β-diversity, community assembly, and ecosystem functioning. Trends Ecol. Evol. *33*, 549–564.

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

OED. (2018a). mangrove, n.1. In OED Online (Oxford University Press). http://www.oed.com/view/Entry/113445?redirectedFrom=mangrave.

OED. (2018b). White man’s grave. In OED Online (Oxford University Press). http://www.oed.com/view/Entry/228621?redirectedFrom=white+man%27s+grave.

Oguibe, O. (2013). I Am Bound to the Land by Blood: Collected Poems (Uhie).

Olesen, J.M., Bascompte, J., Dupont, Y.L., and Jordano, P. (2007). The modularity of pollination networks. Proc. Nat. Acad. Sci. U S A *104*, 19891–19896.

Olyarnik, S.V., and Stachowicz, J.J. (2012). Multi-year study of the effects of *Ulva* sp. Blooms on eelgrass *Zostera marina*. Mar. Ecol. Prog. Ser. *468*, 107–117.

Orwell, G. (1945). Animal Farm: A Fairy Story (Secker and Warburg).

Orwig, D.A., Barker Plotkin, A.A., Davidson, E.A., Lux, Hl, Savage, K.E., and Ellison, A.M. (2013). Foundation species loss affects vegetation structure more than ecosystem function in a northeastern USA forest. PeerJ *1*, e41.

Orwig, D., Foster, D., and Ellison, A. (2015). Harvard Forest CTFS-ForestGeo mapped forest plot since 2014. Harv. Forest Data Archive, HF253. https://dx.doi.org/10.6073/pasta/37e265a91de87b428ccbac8044b124d8.

Otto, S.P., and Day, T. (2007). A Biologist’s Guide to Mathematical Modeling in Ecology and Evolution (Princeton University Press).

O’Brien, J.M., and Scheibling, R.E. (2018). Turf wars: competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. Mar. Ecol. Prog. Ser. *590*, 1–17.

Page, S.E. (2010). Diversity and Complexity (Princeton University Press).

Paine, R.T. (1966). Food web complexity and species diversity. Am. Nat. *100*, 65–75.

Patten, B.C. (1959). An introduction to the cybernetics of the ecosystem: the trophic-dynamic aspect. Ecology *40*, 221–231.

Peters, D.P.C., and Yao, J. (2012). Long-term experimental loss of foundation species:

consequences for dynamics at ecotones across heterogeneous landscapes. Ecosphere *3*, 27.

Petraitis, P.S., and Dudgeon, S. (2005). First year demography of the foundation species, *Ascophyllum nodosum*, and its community implications. Oikos *109*, 405–415.

Pillai, P., and Gouhier, T.C. (2019). Not even wrong: the spurious measurement of biodiversity's effects on ecosystem functioning. Ecology. https://doi.org/10.1002/ecy.2645.

Poe, M.R., Norman, K.C., and Levin, P.S. (2014). Cultural dimensions of socioecological systems: key connections and guiding principles for conservation in coastal environments. Conserv. Lett. *7*, 166–175.

Poelman, E.H., and Kessler, A. (2016). Keystone herbivores and the evolution of plant defenses. Trends Plant Sci. *21*, 477–485.

Poisot, T., Stouffer, D.B., and Kéfi, S. (2016). Describe, understand and predict: why do we need networks in ecology? Funct. Ecol. *30*, 1878–1882.

Preston, F.W. (1948). The commonness and rarity of species. Ecology *29*, 254–283.

Proffitt, C.E., Chiasson, R.L., Owens, A.M., Edwards, K.R., and Travis, S.E. (2005). *Spartina alterniflora* genotype influences facilitation and suppression of high marsh species colonizing an early successional salt marsh. J. Ecol. *93*, 404–416.

Rabinowitz, D. (1981). Seven forms of rarity. In The Biological Aspects of Rare Plant Conservation, H. Synge, ed. (John Wiley & Sons), pp. 205–217.

Record, S., McCabe, T., Baiser, B., and Ellison, A.M. (2018). Identifying foundation species in North American forests using long-term data on ant assemblage structure. Ecosphere *9*, e02139.

ReefBase. (2018). ReefBase – a global information system on coral reefs, Available online: http://www.reefbase.org/global_database/default.aspx.

Ruocco, M., Marin-Guirao, L., Ravaglioli, C., Bulleri, F., and Procaccini, G. (2018). Molecular level responses to chronic versus pulse nutrient loading in the seagrass *Posidonia oceanica* undergoing herbivore pressure. Oecologia *188*, 23–39.

Sala, N.M., Bertness, M.D., and Silliman, B.R. (2008). The dynamics of bottom-up and top-down control in a New England salt marsh. Oikos *117*, 1050–1056.

Schiel, D.R. (2006). Rivers or bolts? When single species count in the function of temperate rocky reef communities. J. Exp. Mar. Biol. Ecol. *338*, 233–252.

Schoener, T.W. (1983). Field experiments on interspecific competition. Am. Nat. *122*, 240–285.

Schuldt, A., Assmann, T., Brezzi, M., Buscot, F., Eichenberg, D., Gutknecht, J., Härdtle, W., He, J.-Sh., Klein, A.-M., Kühn, P., et al. (2018). Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nat. Commun. *9*, 2989.

Schutte, V.G.W., and Byers, J.E. (2017). Variation in a simple trait of mangrove roots governs predator access to, and assemblage composition of, epibiotic sponges. Mar. Ecol. Prog. Ser. *573*, 15–23.

Short, F., Carruthers, T., Dennison, W., and Waycott, M. (2007). Global seagrass distribution and diversity: a bioregional model. J. Exp. Mar. Biol. Ecol. *350*, 3–20.

Solomon, M. (2006). Norms of epistemic diversity. Episteme *3*, 23–36.

Spalding, M., Kainuma, M., and Collins, L. (2010). World Atlas of Mangroves (Earthscan).

Stauffer, H.B., Ralph, C.J., and Miller, S.L. (2004). Ranking habitat for marbled murrelets: new conservation approach for species with uncertain detection. Ecol. Appl. *14*, 1374–1383.

Thomsen, M.S., Wernberg, T., Altieri, A., Tuya, F., Gulbransen, D., McGlathery, K.J., Holmer, M., and Silliman, B.R. (2010). Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integr. Comp. Biol. *50*, 158–175.

Thomsen, M.S., Hildebrand, T., South, P.M., Foster, T., Siciliano, A., Oldach, E., and Schiel, D.R. (2016). A sixth-level habitat cascade increases biodiversity in an intertidal estuary. Ecol. Evol. *6*, 8291–8303.

Thomsen, M.S., Altieri, A.H., Angelini, C., Bishop, M.J., Gribben, P.E., Lear, G., He, Q., Schiel, D.R., Silliman, B.R., South, P.M., et al. (2018). Secondary foundation species enhance biodiversity. Nat. Ecol. Evol. *2*, 634–639.

Tilman, D., Isbell, F., and Cowles, J.M. (2014). Biodiversity and ecosystem functioning. Ann. Rev. Ecol. Evol. Syst. *45*, 471–493.

Tomback, D.F., Resler, L.M., Keane, R.E., Pansing, E.R., Andrade, A.J., and Wagner, A.C. (2016). Community structure, biodiversity, and ecosystem services in treeline whitebark pine communities: potential impacts from a non-native pathogen. Forests *7*, 21.

Ulrich, W., Ollik, M., and Ugland, K.I. (2010). A meta-analysis of species-abundance distributions. Oikos *119*, 1149–1155.

Uriarte, M., Canham, C.D., Thompson, J., and Zimmerman, J.K. (2004). A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. Ecol. Monogr. *74*, 591–614.

USGS (United States Geological Survey). (2016). National gap analysis Project (GAP): mission. https://gapanalysis.usgs.gov/about-gap/mission/.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Coccuci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., et al. (2015). Beyond species loss: the extinction of ecological interactions in a changing world. Funct. Ecol. *29*, 299–307.

Valls, A., Coll, M., and Christensen, V. (2015). Keystone species: toward an operational concept for marine biodiversity conservation. Ecol. Monogr. *85*, 29–47.

Verdu, M., and Valiente-Banuet, A. (2008). The nested assembly of plant facilitation networks prevents species extinctions. Am. Nat. *172*, 751–760.

Williams, R.J., and Martinez, N.D. (2000). Simple rules yield complex food webs. Nature *404*, 180–183.

Wyse, S.V., Burns, B.R., and Wright, S.D. (2014). Distinctive vegetation communities are associated with the long-lived conifer *Agathis australis* (New Zealand kauri, Araucariaceae) in New Zealand rainforests. Aust. Ecol. *39*, 388–400.

van der Zee, E.M., Angelini, C., Govers, L.L., Christianen, M.J.A., Altieri, A.H., van der Riejden, K.J., Silliman, B.R., De Koppel, J.V., van der Geest, M., van Gils, J.A., et al. (2016). How habitat-modifying organisms structure the food web of two coastal ecosystems. Proc. R. Soc. B *283*, 20152326.

Zhao, M.X., Brofeldt, S., Li, Q.H., Xu, J.C., Danielsen, F., Laessoe, S.B.L., Poulsen, M.K., Gottlieb, A., Maxwell, J.F.F.F., and Theilade, I. (2016). Can community members identify tropical tree species for REDD plus carbon and biodiversity measurements? PLoS One *11*, e0152061.