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Interactions among Foundation Species and Their Consequences for Community Organization, Biodiversity, and Conservation

CHRISTINE ANGELINI, ANDREW H. ALTIERI, BRIAN R. SILLIMAN, AND MARK D. BERTNESS

Foundation species create complex habitats in which associated organisms find refuge from biological and physical stress; these foundation species are thus fundamental to the structure and resilience of terrestrial and marine ecosystems. In the present article, we develop an approach to understanding foundation species' effects in communities that are maintained not by a single foundation species, as has been the focus of research to date, but by multiple, co-occurring foundation species. Using examples from diverse ecosystems, we illustrate the prevalence of multiple-foundation-species assemblages and hypothesize that the nature of foundation-species interactions has important consequences for community structure. We predict where positive and negative interactions among foundation species will occur and suggest that they organize communities hierarchically in nested or adjacent assemblages that underlie landscape-scale patterns in species distribution. Elucidating the predictable nature of foundation-species interactions may be key to understanding and managing the biodiversity and functioning of many ecosystems.

Keywords: biodiversity, biogenic habitat, ecosystem engineer, positive interaction, stress gradient hypothesis

Ecologists have long recognized the role of foundation species in facilitating whole communities of organisms through habitat creation (Dayton 1972, Bertness and Callaway 1994, Stachowicz 2001, Ellison et al. 2005). Kelps, conifers, and corals, for instance, are spatially dominant organisms whose biogenic structure promotes species coexistence through the amelioration of physical stress and the creation of fine-scale, complex matrices in which smaller organisms find refuge from predators and competitors (Dayton 1972, Stachowicz 2001). Foundation species are often primary producers and play central roles in sustaining ecosystem services, such as nursery habitats for fish (Boesch and Turner 1984, Carr 1989, Beck et al. 2001), shoreline stabilization (Orth et al. 2006, Koch et al. 2009), water filtration (Altieri and Witman 2006), timber production, and carbon sequestration (Ellison et al. 2005). Because of the economic value of these services and the link between foundation species and biodiversity, recent conservation strategies have prioritized protecting and restoring foundation species in degraded ecosystems (Byers et al. 2006, Crain and Bertness 2006, Halpern et al. 2007, Gómez-Aparicio 2009).

To date, most of our understanding of how foundation species affect community organization and biodiversity has emerged from studies of marine ecosystems in which the

facultative effects of a single dominant, structure-forming space holder have been investigated. In coastal soft-sediment habitats, for instance, extensive beds of the seagrass *Thalassia testudinum* can cover otherwise low-productivity sand flats occupied by algae. By reducing water flow, modifying the substrate, and impeding the foraging efficiency of mobile predators, seagrass beds facilitate the settlement of benthic invertebrates and enhance the survivorship and density of prey species (Orth et al. 1984, Heck et al. 2003, Canion and Heck 2009). Similarly, along thousands of kilometers of Caribbean coastline, networks of red mangrove (*Rhizophora mangle*) roots provide essential nursery habitat for juvenile snappers, grunts, barracuda, and other fishes and physically guard these populations from larger predators (Beck et al. 2001, Faunce and Serafy 2008). Consequently, the trophic dynamics associated with seagrass and mangrove communities arise largely from the biogenic framework provided by foundation species, which suggests a hierarchical community organization in which species and their interspecific interactions occur within a community that is itself established with the facilitation of a foundation species (Bruno and Bertness 2001). Field experiments in which the presence of foundation species was manipulated or their physical attributes mimicked have elucidated the mechanisms by

which foundation species influence the distribution of associated organisms (e.g., shading by nurse plants, Turner et al. 1966; substrate stabilization by cordgrass, Altieri et al. 2007; and nursery effects of mangroves, Laegdsgaard and Johnson 2001). These studies have prompted the revision of general models of community organization that previously emphasized predation, disturbance, and competition (Levin and Paine 1974, Menge and Sutherland 1987) to include positive (i.e., facilitative) interactions. In particular, recognition of the pervasive role of facilitation in communities has given rise to the stress gradient hypothesis (SGH; Bertness and Callaway 1994) and to modified predictions made by the fundamental-niche, intermediate-disturbance, and diversity-invasion hypotheses (Bruno et al. 2003) and has provoked comprehensive reviews of facilitative interactions in a wide range of ecosystems (Callaway 1995, Stachowicz 2001, Maestre et al. 2009).

Although field studies, models, and syntheses have improved our understanding of the central role that foundation species play in structuring communities, our current approach of examining a given foundation species in isolation or by lumping multiple foundation species into a single functional entity overlooks a key characteristic of community organization. Specifically, most ecosystems are structured by multiple foundation species, whose differences in structural and functional morphology influence their community impact (Bruno and Bertness 2001). Seagrass meadows are frequently mixed stands of *Thalassia*, *Zostera*, and *Enhalus* species, which vary in their structural characteristics and functional traits (Duarte et al. 2000); coral reefs are composed of multiple encrusting and branching clonal

organisms, whose growth forms operate in concert to form complex biogenic reef structures and to promote species diversity (Knowlton and Jackson 2001); Costa Rican cloud forests intermix palm- to bamboo-dominated communities with increasing altitude, with cascading effects on associated flora and fauna (Kappelle et al. 1995); and mixed stands of Australian kelp are more common and harbor more diverse benthic assemblages than do monospecific patches (Irving et al. 2003, Goodsell et al. 2004). Despite the prevalence of multiple foundation species and the importance of species-specific traits in modifying habitats, the effects of foundation-species assemblages on habitat complexity or on the spatial distribution, composition, and persistence of higher trophic levels have been evaluated in few studies (box 1).

In one of these few studies in which the coexistence of foundation species was explicitly evaluated, Altieri and colleagues (2007) examined the interactions among foundation species and tested whether they had additive or redundant roles in facilitating New England cobble-beach communities. They found that the foundation species, cordgrass (*Spartina alterniflora*), could independently colonize the shore and facilitate the establishment of ribbed mussel (*Geukensia demissa*) beds within its biogenic matrix by stabilizing and shading the substrate. Established mussels further buffered evaporative stress and generated a hard substrate, which resulted in a higher abundance of species that depend on rigid, stable surfaces (e.g., algae, barnacles, blue mussels) relative to cobble areas without cordgrass and mussels (Altieri et al. 2007). In addition to the abundance of associated organisms, the diversity and overall stability of the cobble-beach community are maintained through

Box 1. Causes for the conceptual oversight of multiple-foundation-species effects.

A wide variety of ecosystems are characterized by multiple foundation species but have not traditionally been described or managed as such because of the scale at which ecologists typically conduct experiments, inconsistent use of terms associated with foundation species, and infrequent application of this concept in studies outside of marine ecology (Ellison et al. 2005). The spatial scale of experiments often leads to the oversight of multiple foundation-species effects, because (a) foundation species are distributed widely across ecosystems, as in mangrove forests and salt marshes, in which multiple species are arranged in broad zones of dominance and experiments are done on smaller spatial scales within zones, or because (b) experiments are conducted entirely within a community defined by a foundation-species assemblage and the interactive effects of habitat-modifying foundation species are not considered (Altieri et al. 2007).

Terminology problems have also diluted the focus on foundation-species effects. Dayton (1972) coined the term *foundation species* nearly four decades ago, but widespread use of similar terms, such as *dominant species* (Grime 1987) and *ecosystem engineer* (Jones et al. 1997) has blurred the concept. In addition to being both *dominant species* (productive organisms that garner a disproportionate share of resources and competitively exclude subordinate species) and *autogenic ecosystem engineers* (organisms that change abiotic and biotic conditions through their own physical structure), foundation species have strong, positive effects on many other organisms in the community. We use the term *foundation species* because it has historical precedence and identifies a class of organism without which the associated biological community would not persist. In addition, many ecologically important, structure-generating organisms are often not recognized as foundation species. Because we have defined *foundation species* as organisms that provide structure; moderate local biotic and abiotic conditions; and have a large, positive effect on other species in a community (Dayton 1972), clams that provide a hard substrate for the attachment of sessile invertebrates within soft sediment habitats (Gribben et al. 2009) and arboreal epiphytes, such as Bird's Nest ferns (*Asplenium nidus*), which harbor diverse invertebrates from predation and physical stress (Ellwood and Foster 2004), are considered foundation species. As a result of these types of oversight, the prevalence and importance of assemblages of multiple foundation species has been vastly underestimated.

facilitation cascades in which an independent, stress-tolerant foundation species (e.g., cordgrass) facilitates a second, dependent foundation species (e.g., ribbed mussels) to provide complementary levels of complexity (i.e., small and large crevices, hard and soft substrates) and to enhance stress amelioration (Altieri et al. 2010). The regularity with which foundation-species distributions overlap suggests that emergent effects, such as facilitation cascades, may play a critical role in the organization and stabilization of many communities (Yakovis et al. 2008).

Coexisting foundation species also compete for space and limited resources. Although many studies have demonstrated competition between dominant, habitat-forming space holders (e.g., tropical forests, coral reefs, salt marshes), how competitive interactions among foundation species influence habitat complexity, diversity, and community organization have been quantified or inferred in relatively few. In the present article, we examine the following questions: (a) Under what conditions do foundation species coexist? (b) What mediates the strength and direction of foundation-species interactions? And (c) does variation in the nature and strength of foundation-species interactions generate predictable landscape-scale patterns in habitat complexity and the distribution of associated species? We use the SGH (Bertness and Callaway 1994) as a conceptual framework to explore these questions, because it has been well supported by studies conducted in a wide range of ecosystems (Bruno et al. 2003). We conclude by discussing how a multiple-foundation-species perspective could enhance the success of future conservation efforts.

Coexistence of foundation species

As space holders that generate and modify habitats, foundation species dominate available substrates in most environments and can coexist at stable population densities (Chesson 2000) in either nested or adjacent assemblages (figure 1). Nested foundation-species assemblages occur when (a) the first foundation species to colonize a habitat does not monopolize the substrate, which enables the colonization of a second foundation species in the interstitial space (i.e., saguaro cacti within a nurse shrub matrix [Turner et al. 1966], mussels within seagrass [Valentine and Heck 1993], clams within macroalgal beds [Gribben et al. 2009]), or (b) the first foundation species to colonize a habitat provides a novel substrate for colonization by and the survival of other foundation species (i.e., tree limbs that host arboreal bromeliads and ferns in neotropical forests [Matelson et al. 1993]; sponges that bind and stabilize rubble to mediate coral attachment and reef growth [Wulff 1984]; and large, foliose brown seaweeds that host a diversity of epiphytic algae [Hay 1986]). In both types of nested assemblages, the initial modification provided by the first foundation species to colonize a habitat allows for the settlement and success of foundation species that would not otherwise occur under ambient environmental conditions. After the foundation species are established, the magnitude and form of habitat

modification (e.g., predator refuge, moisture retention, light regulation) provided by coexisting foundation species is typically complementary and differs as a function of species-specific traits (Irving and Bertness 2009). For instance, palo verde trees buffer the evaporative stress on the obligate foundation species, saguaro cacti, in the Sonoran Desert (Turner et al. 1966) but contribute far less than cacti as a water and nutrient resource or predation refuge for associated birds and invertebrates (Wolf and del Rio 2003). In contrast to classical facilitative interactions, in which one organism directly enhances the success of another, facilitation among foundation species drives whole-community development

Hierarchical organization of communities

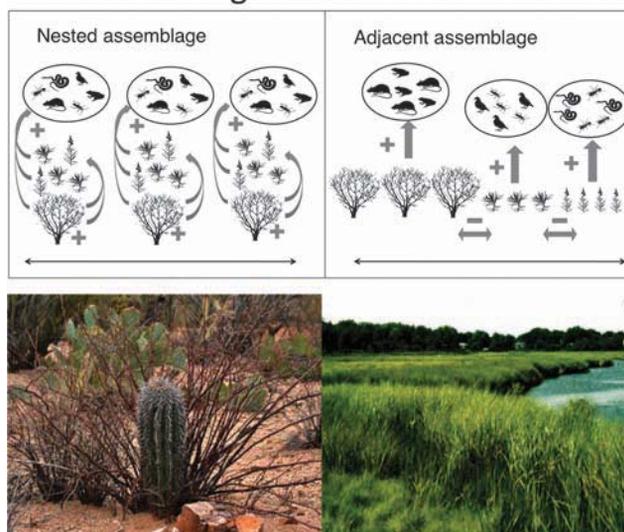


Figure 1. Foundation species may form nested (upper left panel) or adjacent (upper right panel) assemblages. In nested assemblages, positive interactions hierarchically structure communities in facilitation cascades in which the first foundation species to colonize a habitat facilitates other foundation species, and through complementary structural complexity, they support diverse species assemblages. In adjacent assemblages, foundation species compete for space to form discrete competitively determined zones, in which structural complexity is mediated locally by the dominant foundation species and drives variation in community composition across the zones. In both nested and adjacent assemblages, multiple foundation species are needed in order for diverse communities to be supported and for higher-order interactions to be maintained at landscape scales. Nested assemblages are apparent in the Sonoran Desert, where shading and nutrient deposition by nurse shrubs facilitate the growth of saguaro, and the adjacent assemblages of salt marsh grasses are a striking feature along wave-protected New England shorelines. Photo credits: Libby Drumm (*Carnegiea gigantea*, bottom left panel) and Andrew H. Altieri (*Spartina alterniflora*, bottom right panel).

by generating habitats with multiple levels of structure and diverse resources.

In other cases, foundation-species assemblages coexist at large scales across adjacent habitats. Adjacent foundation species occur when a foundation species monopolizes areas of the primary substrate and inhibits colonization by other foundation species that are unable to utilize the interstitial space or the novel substrate created by the dominant foundation species. These adjacent assemblages are most apparent in patterns of foundation-species zonation that occur when ecosystems are viewed at the landscape scale, such as hardwood and conifer zones on mountainsides (Kappelle et al. 1995, Hsieh et al. 1998) and red, black, and white mangroves that border one another on tropical coasts (Sousa et al. 2007). Within each zone, the competitively dominant foundation species locally mediates the complexity of the habitat and drives variation in its structural attributes, such as canopy height, crevice size or substrate conditions, and community composition across space. As in nested assemblages, the diversity and abundance of associated organisms are also promoted at the landscape level, where multiple adjacent foundation species persist.

The strength and direction of foundation-species interactions

Although foundation species are distinguished as a special class of organism (box 1; Dayton 1972), they are ultimately limited by physical or biological stresses or disturbances (e.g., competition, predation), as are all species (Levin and Paine 1974, Menge and Sutherland 1987). Consequently, we anticipate that patterns in the strength and direction of foundation-species interactions mirror classic ecological interactions among species that are not foundation species. The SGH (Bertness and Callaway 1994) predicts that species interactions are negative (competitive) at intermediate levels of physical stress, at which many basal species are able to tolerate environmental conditions and limit the availability of resources, and that positive (facilitative) interactions are more prevalent in either more physically harsh environments, in which neighborhood buffering maintains community structure, or in less physically stressful areas, in which associational defenses play a significant role because of strong consumer pressure (Hay 1986, Bertness and Callaway 1994). Accordingly, we propose that facilitation is the dominant interaction in multiple-foundation-species assemblages, in which the structure of a primary, stress-tolerant foundation species creates a new buffered habitat in which other, obligate foundation species can proliferate, and competition among foundation species is most important when a number of species can act as primary space holders (box 2).

Facilitation. Where might facilitation be the dominant interaction among foundation species if they are—by definition—dominant, habitat-forming organisms vying for space? The SGH predicts that facilitation should be preva-

lent in environments with strongly limiting physical factors, such as high evaporative or wave stress and low nutrient or water availability (Bertness and Callaway 1994) and in which the first foundation species to colonize a habitat experiences limited productivity and therefore cannot completely dominate the space. In stress-maintained interstitial space, less-tolerant foundation species may opportunistically proliferate because of the initial habitat modification by the first foundation species. For example, *Acacia drepanolobium* trees can persist independently in dry Kenyan savannas, although their productivity is restricted by a combination of stress factors, including low precipitation, fires, and heavy browsing by grazers (Riginos et al. 2009). Once they are established, *Acacias* facilitate prairie grass survival and productivity by locally reducing evapotranspiration, increasing water availability through hydraulic lift, and enriching soil nutrients through litter fall (Belsky 1994). Therefore, by suppressing the dominance of the first foundation species to colonize a habitat and opening up space, elevated physical stress can organize communities into nested hierarchical assemblages in which additional foundation species and their facilitative effects are obligately dependent on the first foundation species that colonized the habitat. Furthermore, the spatial arrangement of foundation species in nested assemblages will likely attenuate through communities and drive predictable patterns in the distribution of associated organisms that tend to congregate where structural complexity and resource availability (i.e., crevice size, light, nutritional resources) are highest (figure 1).

The SGH also proposes that facilitation plays a critical role in structuring communities at the opposite end of the environmental stress gradient, where biological stress is high (Bertness and Callaway 1994). According to the Menge–Sutherland community regulation model (Menge and Sutherland 1987), the productivity and food-web complexity of a community increase as physical stress decreases, which results in elevated consumer pressure and stronger suppression of the abundance and distribution of primary producers where physical stress is low. Facilitation emerges in physically benign environments when resident species seek shelter within the matrix of foundation species that are functionally resistant to consumers because of their structural (e.g., calcium carbonate skeletons, thorns, fibrous or woody tissues) or chemical (e.g., alkaloids, terpenoids, phenolics) defenses. Although the facilitative interactions among refuge-providing and refuge-dependent species have been widely recognized (e.g., mangrove roots buffer predation on juvenile fishes [Beck et al. 2001], unpalatable herbs protect palatable neighboring plants from livestock grazers [Callaway et al. 2005]), the ways in which associational defenses might influence coexisting foundation species has received little attention. In environments of low physical stress, in which consumer pressure and the competition among dominant space holders are predicted to be intense (Menge and Sutherland 1987), foundation species that are able to colonize the habitat and exclude other space holders

Box 2. The ecological theater and the evolutionary play: The context dependence of foundation-species interactions.

We propose *nested* and *adjacent assemblages* as distinct types of hierarchical organization that structure communities by facilitative or competitive interactions, respectively. In practice, however, interactions among foundation species are context dependent, varying spatially across landscapes (van Wesenbeeck et al. 2007, Riginos 2009) and temporally over foundation-species ontogenies or fluctuations in their productivity (McAuliffe 1984, Hay 1986) and, therefore, do not necessarily fall neatly into these categories. In any ecosystem (e.g., savannas, cloud forests, coral reefs), a pool of potential space holders exists, and local biotic and physical conditions determine whether dominant species exclude the rest of the pool or whether stress-tolerant species take hold and facilitate the growth of others. Consequently, the same foundation species that interact to form nested assemblages under some conditions may be organized through competitive hierarchies under different conditions.

Case example 1. Hydrodynamic forces (wave exposure and wind stress) vary along the New England coastlines, and it has been shown in field experiments that they drive predictable patterns in the strength and direction of the interactions among primary space holders (van Wesenbeeck et al. 2007). Under high hydrodynamic stress, vegetated cobble-beach communities prevail in which stress-tolerant cordgrass positively interacts with secondary space holders (e.g., forbs, grasses, sedges) to sustain diverse plant communities. Along wave-protected coasts, however, competitive interactions predominate, and inferior sedges and forbs become excluded by stress-intolerant but competitively superior grasses. As a result, distinct community types with unique spatial structures (e.g., vegetated cobble beach, fringing marsh, salt marsh) arise across hydrodynamic gradients because of variation in the strength and nature of the interactions among foundation species, despite a common species pool across all habitats (figure 2).

Case example 2. In the heavily-grazed, arid Nigerian Sahara, interactions between *Acacia tortilis* var. *raddiana*, a leguminous tree that improves soil nitrogen availability and provides protection against soil erosion, and the dense nurse tussock *Panicum turgidum*, which facilitates a diverse assemblage of desert forbs and herbs (Anthelme et al. 2007), shift from a facilitative to a competitive interaction as *Acacia* trees progress from early life stages to mature adult trees. As seedlings, *Acacia* growing alone are browsed intensively by livestock, but those that germinate within the complex matrix of grazer-resistant *Panicum* often persist and continue to grow, which suggests that the associational defenses provided by the tussocks are critical to the establishment of this economically important foundation species (Anthelme and Michalet 2009). As *Acacia* mature and become less vulnerable to grazers, they compete with *Panicum* for water, however, and can limit grass biomass (Ludwig et al. 2004). In this example and potentially many other ecosystems in which consumers selectively browse young and vulnerable species, the associational defenses provided by grazer-resistant foundation species may be essential to the long-term stability of the community and a provision of key ecosystem services.

Since the physical and biotic environment can moderate the strength and even reverse the direction of foundation-species interactions, identifying the environmental context in which foundation species coexist is of central importance to predicting the nature of the community's hierarchical organization. Furthermore, this perspective emphasizes that climate change, which may alter environmental gradients or the anthropogenic modification of natural grazer regimes through activities such as overfishing or intensive livestock grazing, can fundamentally alter the dynamics among habitat-forming dominant species, with cascading effects on dependent organisms.

can support other foundation species that are more susceptible to being consumed or that are inferior competitors by providing a novel substrate for colonization. For example, in Neotropical forests, tree limbs commonly provide the substrate for structurally complex and productive epiphytic ferns and tank bromeliads that are poor competitors for space and vulnerable to grazing and litter suppression on the ground (Matelson et al. 1993) but that are key facilitators of arthropod communities in forest canopies (Ellwood and Foster 2004). Similarly, in temperate macroalgae ecosystems, chemically defended brown seaweeds (*Sargassum filipendula* and *Padina vickersiae*) provide an essential substrate for the attachment of more palatable epiphytic algae (e.g., *Hypnea*, *Ulva*, and *Chondria* spp.; Hay 1986) that secondarily host a range of invertebrates, including sponges, tunicates, crabs, and isopods. Within these structurally dynamic tree-epiphyte and seaweed-algae communities, a rich fauna thrives (Hay 1986, Kitching 2001), despite high ambient consumer pressure in the ecosystem, which illustrates how nested hierarchical foundation-species assemblages may

generate and maintain biodiversity hotspots within an ecosystem (figure 1).

Competition. In habitats experiencing intermediate levels of physical stress, competition—rather than facilitation—among foundation species tends to dominate, because the productivity of the foundation species is higher, which limits the availability of unoccupied, interstitial space for secondary organisms and therefore escalates competition among primary space holders, and because consumer pressure, which is still limited by physical stress, is too weak to mediate foundation-species interactions. Where physical stress is strong enough to exclude some potential foundation species but varies across the community, foundation species are often distributed in adjacent monospecific zones, in which each is a primary space holder and maintains local dominance because of species-specific trade-offs in competitive ability and stress tolerance. Such gradients in environmental stress, such as wave energy along coastlines or moisture and temperature variation across altitudes, are ubiquitous

in natural environments and create an underlying basis for foundation-species segregation (Crain and Bertness 2006). In New England salt marshes, for example, inverse gradients in inundation stress and nutrient availability segregate multiple foundation species (*Spartina alterniflora*, *Juncus gerardi*, and *Spartina patens*) in distinct zones parallel to the shore that are determined by species-specific trade-offs in inundation tolerance and competitive ability (Levine et al. 1998). Likewise, Patagonian rocky intertidal communities are organized by a competitive hierarchy in which the extensive beds of the desiccation-tolerant and competitively inferior mussel *Perumytilus purpuratus* are displaced to physically stressful middle and high intertidal zones, whereas stress-intolerant but competitively dominant coralline algae monopolize the low intertidal zone (Bertness et al. 2006). These two foundation species differ in structural complexity (i.e., the dimensions of interstitial space, thermal buffering), the effects of which cascade up to other organisms, influencing the distribution and abundance of sea stars, limpets, and crustaceans (Hidalgo et al. 2007). In general, we predict that, as has been seen on Patagonian rocky shores, spatial segregation of foundation species along stress gradients gives rise to variation in the composition and functional traits of the associated organisms that selectively congregate near particular foundation species (figure 1). Therefore, persistence of multiple foundation species that facilitate different suites of organisms is likely critical to maintaining overall species diversity and community stability.

The effects of foundation-species diversity and habitat complexity on biodiversity

The interactions among foundation species have cascading effects on the diversity and abundance of their associated organisms. By providing a variety of refuge sizes, substrates, and microclimates, multiple foundation species add additional levels of habitat complexity (Altieri et al. 2007), which in turn mediates niche availability and predator-prey and competitive dynamics. Whether foundation species exist in nested or adjacent assemblages, however, will determine whether their combined effect is enhanced local diversity brought on by the overlapping of the foundation species or is enhanced cumulative diversity over larger scales when species' distributions are segregated by adjacent foundation species (figure 1). In addition, foundation-species productivity will have important implications for the strength of habitat modification (species with more biomass should be stronger modifiers) and will thus have the potential to facilitate other foundation species or associated organisms.

Conclusions

Over decades of research, biogenic habitat creation by single foundation species has been emphasized (Dayton 1972). Here, we revise this approach to understanding community organization by developing the idea that multiple foundation species interact in most ecosystems to synergistically

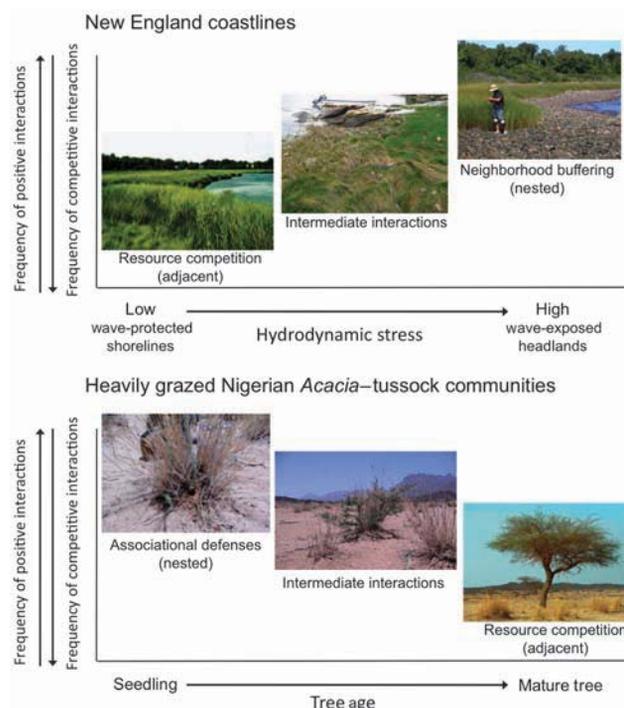


Figure 2. The context dependence of interactions among foundation species. Despite a common pool of species, shoreline community composition varies widely across hydrodynamic stress gradients in New England as a consequence of foundation-species interactions shifting from competitive interactions along wave-protected coasts to facilitative interactions along wave-battered cobble beaches. Likewise, the nurse tussock, *Panicum*, provides a critical refuge for *Acacia* seedlings from grazers in intensively browsed, arid Nigerian landscapes but competes with *Acacia* for water as the trees mature and become less vulnerable to predation. Photo credits: Andrew H. Altieri (salt marsh photos) and Fabien Anthelme (desert photos).

structure communities, to enhance species diversity, and to stabilize ecosystem function. We suggest that future investigators of community assembly consider the hierarchical organization of foundation species; the strength and direction of their interactions; and the structural complexity of habitats that arise from their presence, persistence, and interactions. In addition, acknowledging that adjacent assemblages, which have historically been studied in isolation, may be a predictable outcome of interactions among foundation species exposes the need to adopt landscape-scale perspectives of communities and their underlying stress gradients.

The loss and degradation of foundation species as a result of deforestation, pathogens, depletion of top predators, urban development, climate change, and eutrophication is a widely recognized global problem (Coleman and Williams 2002, Ellison et al. 2005, Altieri and Witman 2006,

Bracken et al. 2007). In addition to strategies to prevent further loss of foundation species, we suggest a more proactive approach to restoration that prioritizes reestablishing foundation-species assemblages to degraded ecosystems as a means to restore stable, diverse communities. In the Nigerian Sahara, for example, intensive livestock browsing is linked to low regeneration of the key leguminous tree, *Acacia tortilis* (Anthelme and Michalet 2009). Anthelme and Michalet (2009) demonstrated that transplanting *Acacia* seedlings within the protective matrix of the naturally abundant nurse tussock (*Panicum turgidum*) increases tree survivorship and growth at vulnerable, early life stages (figure 2). As a result, Anthelme and Michalet (2009) recommended that future conservation efforts utilize natural grazing refuges (e.g., the foundation species *Panicum turgidum*) as a cost-effective solution for enhancing the density of *Acacia* in an effort to restore biogenic structure and ecosystem function in these landscapes. Likewise, the success of seagrass restoration projects in fostering the return of plants and fauna to soft-sediment habitats in Chesapeake Bay might be improved if multiple seagrass species, rather than only *Zostera marina*, were seeded, because it would result in the reestablishment of a complex community structure over relatively short time scales (see Marion and Orth 2010 for details). In general, harnessing facilitation (Byers et al. 2006, Halpern et al. 2007) among naturally synergistic foundation species—not just the presumed competitively dominant species—by planting or seeding should be evaluated as a tool to restore biological communities and ecosystem services in severely degraded habitats.

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