

Mutualism, Facilitation, and the Structure of Ecological Communities

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Facilitative, or positive, interactions are encounters between organisms that benefit at least one of the participants and cause harm to neither. Such interactions are considered “mutualisms” when both species derive benefit from the interaction. Positive interactions are ubiquitous: They may lie at the root of such diverse evolutionary phenomena as the origin of eukaryotic cells, the radiation of flowering plants, and the flourishing of coral reefs. Although a few ecologists have long recognized the importance of positive interactions in stressful environments (e.g., Clements 1916, Addicott 1984), ecological research on positive interactions is still far less common than that on other forms of interactions among species (Bronstein 1994a, Bruno and Bertness 2000). Consequently, positive interactions are rarely factored into models or even into thinking about factors impacting populations and communities. Recent empirical work and the conceptual models derived from this work (e.g., Bertness and Callaway 1994, Bruno and Bertness 2000) have helped refocus attention on the role of positive interactions among species, however, and scientists are beginning to better appreciate the importance of those interactions in the structuring of ecological communities.

Simply by growing, many species alter the local environment. Trees cast shade on the forest floor, altering light and moisture regimes; corals form reefs, increasing habitat complexity and thereby providing habitat for countless other species. Many of the positive interactions that have emerged as important to community structure can be placed into this category of “habitat modification,” in which one individual (or species) alters local environmental conditions, often making a stressful habitat more hospitable for other individuals or species.

I define *stress* broadly, as any extrinsic force that reduces the fitness of an individual or population. Stresses can be physiological (e.g., temperature, salinity, drought conditions), physical (e.g., direct effects of wind, waves, currents), or biotic (e.g., competition, predation, disease). Thus positive interactions occur when one organism makes the local environment more favorable for another either directly (such as by reducing thermal stress via shading or decreasing wind

POSITIVE INTERACTIONS PLAY A CRITICAL, BUT UNDERAPPRECIATED, ROLE IN ECOLOGICAL COMMUNITIES BY REDUCING PHYSICAL OR BIOTIC STRESSES IN EXISTING HABITATS AND BY CREATING NEW HABITATS ON WHICH MANY SPECIES DEPEND

stress via baffling) or indirectly (such as by removing competitors or deterring predators of that species).

Jones and colleagues (1997) have called this process “ecosystem engineering” and the species that modify the habitat “bioengineers.” Although these terms are useful metaphors for the critical role these species play in ecosystems, their use has stirred controversy because, for some, they imply conscious intent on the part of the species doing the “engineering.” Many habitat-modifying species form the basis on which the entire community is built, which led Dayton (1975) to dub them “foundation species,” a term perhaps less laden with anthropomorphic connotations. Bruno and Bertness (2000) proposed that marine benthic communities such as coral reefs, kelp forests, and rocky shores be viewed as being hierarchically organized because they are reliant principally on the presence of “foundation,” or habitat-forming, species (corals or seaweeds, e.g.) (Figure 1). They argue that small-scale interactions among species (both positive and negative) can

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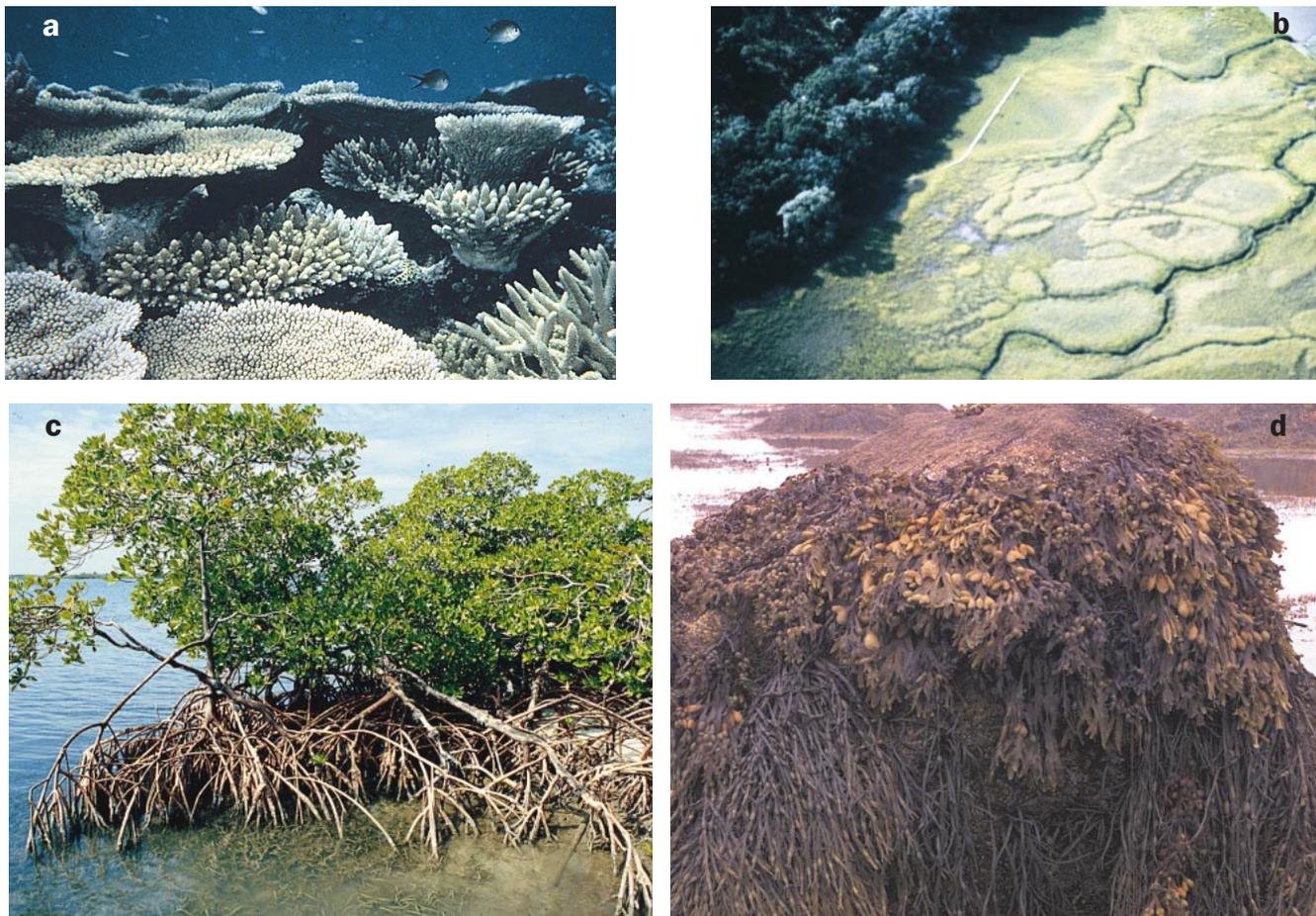


Figure 1. Habitat amelioration and habitat creation as a result of positive interactions. (a) Coral reefs are formed by positive interactions between corals and microalgae (zooxanthellae) and offer shelter from predators as well as waves and currents for a vast diversity of invertebrates and fishes. Some of these animals are herbivores that benefit corals by mediating competition with macroalgae. Photo courtesy of Gian Cetrulo. **(b)** Salt marsh accretion and zonation is attributable in part to positive interactions among plants in the marsh as well as between plants and marine animals such as mussels and fiddler crabs. Photo courtesy of Mark Bertness. **(c)** Mangroves serve as nursery habitats for a diverse assemblage of reef fishes. These trees benefit from a nutrient exchange with sponges growing on their roots in much the same way that mycorrhizal fungi or nitrogen-fixing bacteria benefit plants growing on land. Photo courtesy of Mark Bertness. **(d)** Intertidal seaweeds form canopies that buffer understory organisms from harsh physical conditions during low tide, altering the vertical zonation of organisms commonly observed in these habitats. Photo by J. J. S.

be understood only within the environmental context determined by the habitat-ameliorating effects of these foundation species. These foundation species often depend on the mobile fishes and invertebrates that they shelter to keep them free from their own predators and competitors (Glynn 1976, Duffy 1990, Stachowicz and Hay 1996, 1999a, Miller 1998), which argues for the importance of indirect positive interactions in maintaining these critical habitats. Given that many, if not most, terrestrial habitats also are dominated by foundation species or ecosystem engineers such as trees or grasses (Jones et al. 1997), this idea should be broadly applicable.

Experimental approaches that document the strengths and outcomes of interactions under a range of environmental conditions (e.g., Bertness and Hacker 1994, Menge et al. 1994, Greenlee and Callaway 1996, Bertness and Leonard

1997) have helped to answer the question of whether positive interactions impact communities—and the answer is unequivocally yes. In particular, small-scale interactions involving the local amelioration of a single stress are relatively well known. More poorly understood is the feedback between large- and small-scale positive interactions and the manner in which each of these contributes to patterns of species richness and diversity. Moreover, ecologists know little about how different positive interactions ameliorate different stresses across the range of a single species, or about the evolutionary consequences of being involved in many such interactions.

The purpose of this article is to describe in greater detail what ecologists do and do not know about positive interactions and how they affect populations and communities. To

arrive at the current understanding of these interactions, I review the diversity of mechanisms by which species directly or indirectly benefit each another and discuss the effects of these interactions on the structure of the communities in which they take place. Because of space constraints, I have focused on recent work; interested readers should consult reviews by Boucher and colleagues (1982), Hunter and Aarssen (1988), Bronstein (1994a), and Callaway (1995) for more examples.

The examples in this article are organized by type of stress that is being ameliorated (physical stress, predation, and so on) and by type of organism, either conspecific or heterospecific, that ameliorates that stress. It is important also to understand the effects of the facilitated species on the facilitator itself: Is the interaction mutualistic(+, +), facilitative–commensalistic (+, 0), or antagonistic (+/–)? When species that benefit from the environment provided by foundation species, either directly or indirectly, in turn facilitate the foundation species, the stability of the system may be enhanced. Nevertheless, I do not treat mutualisms, commensalisms, and facilitation separately because any interaction between a single pair of species (or conspecific individuals) can vary in outcome, depending on the environmental context (e.g., Bronstein 1994b).

I conclude by examining two areas in need of further research: the impacts of positive interactions on species diversity and the variation in positive interactions on geographic scales. By considering a diverse suite of direct and indirect positive interactions as a unified group, I hope to encourage a focus on the mechanisms by which species benefit each other and affect community structure and diversity.

Benefits of group living: Intraspecific positive interactions

One of the classic mechanisms through which populations are thought to be regulated is density-dependent mortality. High intraspecific densities can be associated with high rates of mortality because of competition for limiting resources—such as food, light, or space—or increased rates of detection by predators. However, life in large groups also offers less-frequently quantified benefits, such as cooperative defense against predators or enhanced foraging success. Nevertheless, early ecological thought championed the importance of competition in the regulation of populations and communities. This notion led to the prediction that positive intraspecific interactions would occur only where competition is weak. For example, the weak and sporadic nature of competition in marine soft-sediment communities, coupled with their enhanced survival at high densities, has been suggested to select for the evolution of gregarious settlement among infaunal bivalves (Peterson and Black 1993). Even at extremely high densities, mortality from competition is virtually undetectable among suspension feeding bivalves in marine soft-sediment communities (Peterson 1991). High densities of these bivalves physically interfere with the ability of predators to consume them but have little effect on bivalve competition for food or space (Peterson and Black 1993).

Moreover, certain groups of birds, fishes, and mammals more actively cooperate to defend against predators by coordinating behaviors among individuals (Dickman 1992).

However, gregarious behavior also occurs in communities in which competition is often intense—among animals that live on rocky shores and in seaweeds and terrestrial plants, for example. High densities of many terrestrial plants and sessile marine invertebrates reduce the susceptibility of individuals to predators, competitors, or physical stresses during vulnerable juvenile or seedling stages (Buss 1981, Schmitt and Antonovics 1986, Bertness and Yeh 1994). Of course, by definition an interaction can be positive only when the benefits exceed the costs, but competition need not be weak for an interaction to have a net positive outcome. Strong benefits such as increased survival rate can override even intense negative competitive effects on growth, resulting in a net positive interaction even when the costs of coexistence are high.

Groups of organisms may also be better able to withstand physiological stresses than solitary individuals. The upper limit to species' distributions in the marine rocky intertidal zone (Figure 1d) is generally thought to be determined by tolerance of thermal stress or desiccation. Thus, in stressful environments, such as the high intertidal zone, organisms should benefit from living in dense intraspecific stands that buffer them from the physical environment. On shores with a high density of plants and animals, shading by conspecifics renders temperatures less extreme and variable, and evaporation is reduced. However, sufficient thermal buffering is provided only at high conspecific densities; when stands of intertidal mussels, barnacles, or seaweeds are artificially thinned, survival of remaining individuals decreases (Bertness and Leonard 1997). Thermal buffering thus extends the distribution of these species higher into the intertidal zone than would be possible if individuals occurred at lower densities or as solitary individuals. However, the benefits of high-density living are apparent only where heat and desiccation stress are greatest. In the less stressful lower intertidal zone, living in dense aggregations confers no survival advantage but instead exacts a cost in the form of decreased growth rates (Bertness and Leonard 1997). Similarly, seedlings of marsh elders (*Iva frutescens*) survive best in areas where seedling density is high or adult marsh elders (or other adult plants) form a canopy that can reduce evaporation rates and decrease soil salinity (Bertness and Yeh 1994). Yet when water is experimentally added to plots, reducing soil salinity, the presence of neighboring conspecifics strongly depresses plant growth rate.

Community implications of interspecific positive interactions

Although all of the examples discussed thus far involve members of the same species, there is no reason that the mechanisms by which conspecifics benefit each other would not operate for heterospecifics as well. Positive interactions between different species are of particular interest because of their potential to “cascade” throughout the community,

with major effects on the structure and function of ecosystems.

Refuge from physical stresses. The idea that the habitat-modifying effects of one species may benefit other species was championed as an important mechanism of community succession decades ago by early plant ecologists (Clements 1916). Only relatively recently, however, has clear experimental evidence emerged to suggest that this widespread phenomenon has important consequences for the structure and function of natural communities. Terrestrial, aquatic, and marine vascular plants (Figure 1b and 1c), as well as reef-forming corals (Figure 1a) and giant kelps, all help to reduce flow (wind or water) and enhance deposition and stabilization of the substrate, facilitating countless other species intolerant of disturbed conditions. Many different species can play similar habitat-modifying roles within the same community. Some are examples of “whole-community” facilitation: For example, in desert communities, microscopic plants secrete polysaccharides that bind soil particles together, reducing erosion and runoff and enhancing germination of higher plants (West 1990). Similarly, substrate stabilization caused by the buffering of wave action by large (longer than 25 m) beds of the intertidal grass *Spartina alterniflora* facilitates the persistence of an entire community of annual and perennial plants below the high-water mark (Bruno 2000). In both of these communities a single key species (i.e., a “keystone” facilitator, or mutualist) modifies the local physical conditions, enabling the existence of an entire community of other species.

Elevational limits to plant distributions are often set by changing levels of physical stresses (e.g., gradients in temperature, moisture, exposure), so it follows that habitat-

ameliorating interactions could play an important role in extending the vertical limits of species distributions. For example, a series of studies on interspecific interactions among salt marsh plants demonstrated that positive interactions alter elevational patterns of species distribution along a tidal gradient in these habitats (Bertness and Hacker 1994, Hacker and Bertness 1995, 1996). In the upper regions of southern New England salt marshes (Figures 1b and 2), hypersaline soils caused by high rates of evaporation result in stressful conditions for many vascular plants. However, this stress can be ameliorated when salt-tolerant plants provide enough ground cover to shade the soil and reduce evaporation rates. In particular, Bertness and Hacker (1994) showed that the canopy formed by the black needle rush, *Juncus gerardi*, extends the distribution of the marsh elder (*Iva*) seaward, into these potentially more stressful areas. Experimental removal of *Juncus* from around marsh elders at intermediate to high elevations in the marsh (Figure 2) decreases marsh elder growth, increases water stress, and increases mortality of marsh elders relative to those surrounded by *Juncus*. However, under more benign physical conditions (i.e., location at higher elevation in the marsh, where soils are less saline), *Juncus* decreases marsh elder growth by competing for resources. Similarly, at high elevations near the timberline, where physical stresses are intense, firs benefit from association with pines, but the association reduces fir growth under more benign conditions typical of sites at lower elevations (Callaway 1998).

An increasing number of examples demonstrate that certain plant species reduce soil erosion, shade the soil surface and reduce evaporation, or buffer harsh wind or temperature conditions, facilitating the persistence of other species and extending their elevational or geographic range. Examples of this

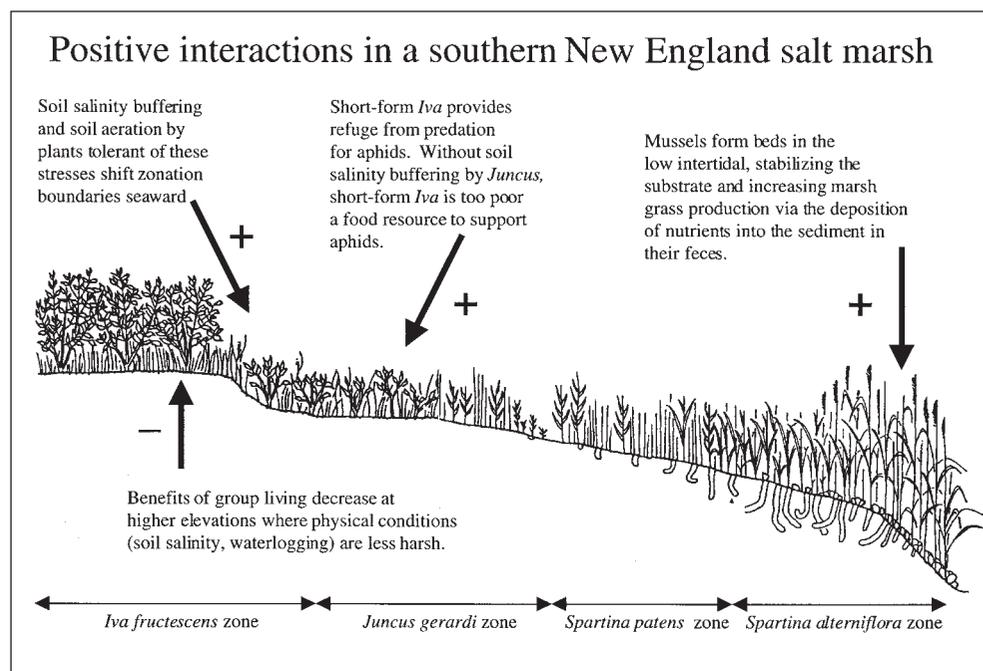


Figure 2. Positive interactions in southern New England salt marsh communities. Figure modified from Bertness and Leonard (1997).

“nurse plant” effect appear to be particularly common in extreme environments, such as deserts (Franco and Nobel 1989) and other areas prone to drought or frost (Ryser 1993). However, the community- and systemwide effects of habitat-ameliorating interactions among plants are still little understood. In eastern US salt marshes, for instance, the persistence of higher trophic levels (herbivore and above) is contingent on the habitat-ameliorating effects of *Juncus*, which allow *Iva* plants to exist in a shorter form in the middle marsh (Figure 2). Aphids benefit from the facilitative effects of *Juncus* in two ways: (1) They use middle-marsh, *Juncus*-associated *Iva* as a refuge from

predation by beetles, which forage almost exclusively on taller plants found higher in the marsh (Hacker and Bertness 1995); and (2) in the middle marsh, aphids survive and reproduce better on plants associated with *Juncus*, which are healthier and nutritionally superior to plants not associated with *Juncus* (Hacker and Bertness 1996). Simple population models indicate that aphids (and perhaps predators that feed on aphids) would become locally extinct within a single growing season in the absence of the positive interaction between *Iva* and *Juncus* (Hacker and Bertness 1996).

Refuge from predation. Species that are resistant to predators may provide “associational refuges” for other species that are susceptible to these predators. Plants in both terrestrial and marine environments that are preferred by herbivores grow faster and suffer less herbivory when associated with un-

palatable plants than when growing alone (Atsatt and O’Dowd 1976, Hay 1986). While the palatable plants clearly benefit from this associational resistance to herbivores, the previously unpalatable host may not if it becomes more attractive to herbivores once it is covered by a palatable epiphyte. Thus some associational refuges may carry a cost to the host; the relationship might even be considered parasitic when the species that is vulnerable to predation becomes too abundant on its host. However, where plants that are resistant to herbivores dominate the community, associational refuges increase overall community species richness by providing safe sites for palatable species (Hay 1986). Mobile organisms can also exploit structural and morphological defenses of plants and sessile animals as a refuge from their own predators. Ants use the swollen thorns of *Acacia* trees as domiciles (Janzen 1966, Beattie 1985); caterpillars roll themselves in the older, rigid leaves of some plants (Dammann 1987); and marine invertebrates shelter from predators within the structurally complex habitat formed by seagrasses, seaweeds, and corals (Peterson 1982, Witman 1987, Stachowicz and Hay 1996, 1999a).

Just as structural complexity provides refuge by physically excluding some predators, noxious antipredator chemicals often deter a wide range of larger consumers and provide local safe sites for smaller animals. By living on or near chemically defended plants that are rarely visited by larger omnivores, some small grazers (e.g., insects, crustaceans, polychaetes, sea slugs) are able to reduce their encounter rates with potential predators (Bernays and Graham 1988, Hay 1992). In many, if not most, of these associations the small grazers are resistant to the chemical defenses produced by its host plant and use the host as both food and shelter; therefore, while the grazer may benefit from the interaction, the plant is harmed. Because such a situation stretches the bounds of “positive” interaction, I omit discussion of much of the literature on specialized plant–herbivore associations, including examples where herbivores physiologically or behaviorally sequester defensive compounds from their prey (Hay 1992, Rowell-Rahier and Pasteels 1992).

However, some species use chemically defended plants as shelter yet feed on other species. For example, decorator crabs cover their carapace with algae or sessile invertebrates as camouflage from predators—and thus never abandon their shelter—but they need not feed on these sheltering species. One species, *Libinia dubia*, practices a form of chemical camouflage (Figure 3a; Stachowicz and Hay 1999b) in which it decorates with the chemically noxious brown alga *Dictyota menstrualis*, rendering itself unpalatable to fishes. The diterpene alcohol produced by the alga to deter herbivores cues decoration behavior in the crab; thus the crabs are, in a sense, behaviorally sequestering seaweed chemical defenses. Predation rates on crabs that do not place chemically noxious algae on their carapaces may be high enough to result in local extinction (Figure 3b). The effects of *Libinia* on *Dictyota* have not been quantified, but algal decorations apparently remain viable. Moreover, they may benefit from access to nutrients from crab excretions and to removal of herbivorous

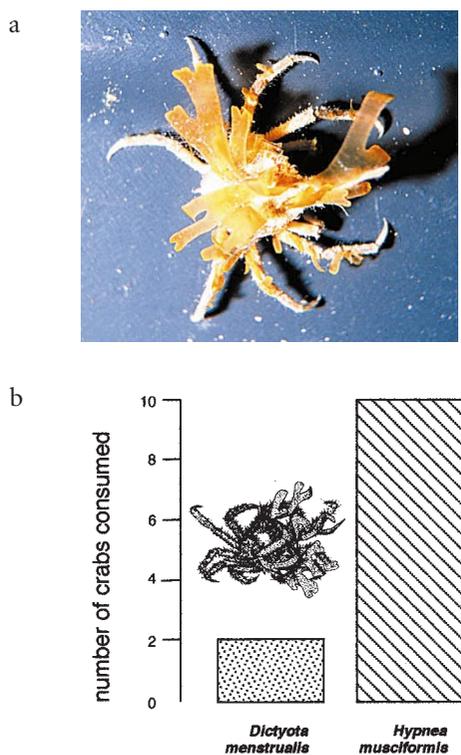


Figure 3. Chemical refuge from predation. (a) The decorator crab (*Libinia dubia*) decorated with brown alga *Dictyota menstrualis*. In coastal North Carolina, the crab covers its carapace with this chemically noxious alga as a form of chemical camouflage from predators. *Dictyota* produces a diterpene alcohol (dictyol E), which protects it from consumption by herbivorous fishes and stimulates decoration behavior in the crab. (b) Because herbivorous fishes also prey on crabs, crabs covered with *Dictyota* survive better in the field than crabs covered with other algae that fishes like to consume. The crabs thus behaviorally sequester the chemical defenses of the alga for use against their own predators without any apparent harm to the alga. Figure modified from Stachowicz and Hay (1999b). Photo by J. J. S.

amphipods by crabs. Similar selective decorating behavior by an Antarctic sea urchin may “rescue” chemically defended seaweeds that have been detached from the substrate, keeping them from being washed ashore or carried beneath the photic zone (Amsler et al. 1999). Because urchins carry reproductive individuals into habitats from which macroalgae has been removed by disturbance, they may also facilitate plant dispersal. These examples highlight the indirect benefits of plant defensive chemicals on some herbivores and illustrate that mutually beneficial interactions can take place between species that might typically be thought of as predator and prey.

Nutrient transfer and trophic facilitation. Probably one of the most well-known and studied group of positive interactions are those between plants and animals that pollinate them or disperse their seeds. Animals typically get a reward for this service: nectar for pollination or fruit for seed dispersal. Intensive study of a few cases of these interactions have significantly advanced our understanding of mutualisms from an evolutionary and population biology perspective (Bronstein 1994a). In particular, studies of these mutualisms have been critical for the realization that interactions that are apparently mutualistic are not always mutually beneficial and that the magnitude of the costs and benefits of the interactions can shift in space and time (Bronstein 1994b). However, relatively few studies directly address the consequences of the removal of the pollinator or the plant on each other and the impact of the pollination or dispersal failure on the community as a whole. Many plant species that appear vulnerable to the loss of a particular pollinator or seed disperser have compensatory mechanisms (self-pollination, alternative pollen vectors, vegetative propagation) that prevent failure (Bond 1994). Nevertheless, when plants with highly specific pollination or seed dispersal requirements perform some critical ecosystem function, the loss of a mutualist could have important ecosystem-level consequences. For example, each species of tropical fig is pollinated by a single tiny wasp species, and the loss of the species-specific pollinator could result in the demise of that species. Because figs provide critical food for a diverse array of birds and mammals during periods of low food abundance, the faunal composition of tropical forests might be radically altered in the absence of the fig-wasp mutualism (Terborgh 1986).

Nutrient acquisition in many terrestrial vascular plants is a result of positive interactions between plant roots and bacteria or fungi in the soil. Mycorrhizal fungi can take up nutrients at particularly low concentrations and pass these along to plants via the roots. Additionally, some plants (mainly legumes) gain nutrients through symbiotic association with bacteria. These plants develop nodules to house the bacteria and provide them with a source of carbon from carbohydrates produced in photosynthesis, while the bacteria make nitrogen biologically available to the plant. However, it is more costly to acquire nitrogen through this association than to obtain inorganic nitrate directly from the soil, so these interactions are beneficial to the plant only in areas of nutrient stress (i.e., low

nitrogen availability). When nitrogen is readily available in the soil, the interaction can actually put the plant at a competitive disadvantage relative to nonsymbiotic neighbors. Similar costs associated with harboring arbuscular mycorrhizal fungi make them advantageous only in areas of nutrient or water stress; indeed, these symbionts may be better classified as parasites for many species of plants (Francis and Read 1995).

Variation in the outcome of host-symbiont interactions among species and within species due to changes in environmental conditions can have dramatic consequences for the structure and composition of plant communities and the animals on which they depend. For example, in prairie grass communities, nutritional benefits derived from mycorrhizal fungi give an advantage to certain tallgrass species, allowing them to become competitively dominant and to exclude other grasses and forbs that derive less benefit from their association with these fungi (Hartnett and Wilson 1999). When mycorrhizal abundance is reduced by applying a fungicide, many previously subordinate species become established, resulting in an increase in local species diversity. Thus, these fungi may act as keystone species in grassland communities by facilitating a competitive dominant rather than by removing it. Even when mycorrhizal fungi do not directly affect the growth of a pair of competing plants, they can alter the outcome of competition between these plants by translocating nutrients among individuals and species, allowing one plant to effectively “parasitize” another. Such an interaction in the western United States between an introduced weedy plant and native grasses facilitates the invasion and spread of the exotic species (Marler et al. 1999). Positive nutritional interactions, including plant-pollinator, plant-fungi, and plant-bacteria interactions (or the lack thereof), have been implicated in the success (or failure) of many introduced species to become established in new habitats (Richardson et al. 2000).

Although mutually beneficial nutritional exchanges are best known among vascular plants, they are by no means restricted to the terrestrial environment. Marine sponges growing on the roots of the red mangrove tree in Belizean mangroves (Figure 1c) perform a role analogous to that played by mycorrhizal fungi on terrestrial plant roots (Ellison et al. 1996). These sponges induce mangroves to produce fine rootlets that bore within the tissues of the sponge, allowing for photosynthetically derived carbon to be transferred from the plant to the sponge and nitrogen derived from ingested zooplankton to move from the sponge to the plant. The exchange is mutually beneficial in the relatively pristine, nutrient-poor waters of Belize, where nitrogen available for plant growth is scarce and may be limiting, but it could become commensal or even parasitic in the more nutrient-rich mangrove systems near developed areas of the coast.

Many bivalve molluscs and sponges form mutually beneficial associations with marine vascular plants, and, given the habitat-ameliorating properties of these plants, these interactions may be of widespread importance for the structure and function of marine communities. For example, Bertness

(1984) showed that nutrients contributed to marsh soils by suspension-feeding mussels, combined with the substrate-stabilizing effects of these mussels, increased marsh grass productivity and enhanced marsh stability and accretion (Figure 2).

Probably the best-known nutritional symbiosis in the marine environment involves the symbiotic relationship between scleractinian (reef-building) corals and dinoflagellate microalgae called zooxanthellae. Many corals receive the bulk of their nutrition from the photosynthate produced by their microalgal symbionts. In turn, the dinoflagellates receive a steady supply of nitrogen from coral waste products. Corals can act as hosts to a multispecies community of algal symbionts. Because each microalgal species appears to be differentially susceptible to environmental stresses such as high light and temperature, multiple symbionts can persist in different microenvironments within a single coral colony (Rowan et al. 1997). This in turn affects intracolony and intercolony variability in exhibiting the stress response known as coral bleaching, in which the algal symbionts are expelled from the host. The short- and long-term community implications of interactions among multiple associates in close-knit positive interactions such as this one should prove an interesting area for future research.

Refuge from competition. While the coral–microalgal symbiosis is undoubtedly important for present day coral reefs (Figure 1a), it is not the only factor responsible for the origin and maintenance of these strongholds of marine biodiversity. Photosynthetic mutualisms do increase rates of reef growth and calcification, yet the fossil record suggests that scleractinian corals acquired photosynthetic symbionts relatively early in their evolutionary history (210 million years ago), which did not immediately confer superior reef-building ability (Wood 1998). The large colonial corals and calcified seaweeds typical of modern reefs showed a high degree of resistance to and resilience from disturbance, but they were poor competitors with fleshy seaweeds for limited substrate in the absence of some disturbance agent. They did not rise to prominence in shallow-water reef communities until the appearance of major groups of herbivorous invertebrates and fishes (Wood 1998).

The role of herbivores in promoting the evolutionary diversification of corals (and vice versa) is still conjectural, but there is strong evidence for such positive interactions among modern species. In well-lit habitats, corals grow slowly relative to seaweeds, and the persistence of tropical coral reefs appears to be linked to the high abundance of herbivores on these reefs, as these herbivores prevent overgrowth of corals by seaweed. When herbivorous fishes or sea urchins are naturally or experimentally removed from these reefs, seaweed biomass increases dramatically and corals are smothered, changing the reef from one dominated by corals to one dominated by fleshy macroalgae (reviewed by Miller 1998). Because the calcium carbonate skeletons generated by living corals are responsible for the growth and maintenance of these reefs, the

replacement of corals by seaweeds may have serious consequences for the long-term persistence of these structures.

When the herbivores that benefit corals by removing algae also use the reef structure as shelter, these interactions may be mutually beneficial. Such is the situation on the shallow warm-temperate reefs of the Carolinas, where seaweeds dominate and generally exclude corals. Here, herbivorous fishes and urchins alter seaweed species composition through selective removal of preferred species, but they do little to diminish total seaweed biomass and are thus unable to mediate coral–algal competition (Miller and Hay 1996). However, one coral (*Oculina arbuscula*) does co-occur with seaweeds on these reefs. It is the only species at this latitude in the western Atlantic to possess a complex, branching morphology that allows it to offer refuge to a diverse suite of smaller invertebrates, including the crab *Mithrax forceps* (Figure 4a). This crab is unusual in that it readily consumes all local seaweeds and is not deterred by chemical defenses that suppress feeding by local fishes, sea urchins, and other crabs. These crabs exhibit low mobility and feed in the immediate vicinity of the coral, creating a halo of reduced seaweed biomass around the coral, dramatically enhancing coral growth and survival by freeing it from competition with seaweeds (Figure 4; Stachowicz and Hay 1999a). By ensuring the persistence of the coral, the crab also indirectly facilitates a diverse epifaunal community of over 300 species within the coral's branches; thus the crab may be thought of as a keystone mutualist in this system. Although these crabs and corals live together throughout their depth range, this cleaning behavior is important only in shallow waters, where seaweeds are common. In deeper waters, where seaweed abundance is low because of low light levels, the corals are not affected by the presence of the crabs, although the crabs still use the coral as a shelter from predators.

A generalization is beginning to emerge: A diverse array of structurally complex but competitively inferior organisms rely on mobile associates to protect them from superior competitors. These cleaning or guarding interactions are common and demonstrably important in maintaining a variety of habitat-modifying organisms, as well as the habitats they create. For example, Littler and colleagues (1995) showed that selective grazing by a chiton on a reef-building coralline alga stimulates meristematic activity in the coralline alga while removing juvenile stages of competitively superior fleshy algae. Consequently, grazing by this chiton increases coralline algal growth and reef accretion. When chitons are removed, filamentous algae overgrow the coralline alga, increasing its palatability to reef fishes and ultimately leading to net erosion of the reef. Similar interactions occur in which sea urchins protect mussels from overgrowth by kelps (Witman 1987), crabs protect reef-building corals from direct predation by the “crown of thorns” starfish (Glynn 1976), and ants protect tropical *Acacia* and *Cecropia* trees from herbivores and competing plants (Janzen 1966, Beattie 1985). Because the carbonate skeletons of corals and other calcified organisms and the woody stems of trees provide the biogenic habitat complexity upon which many other species depend, positive

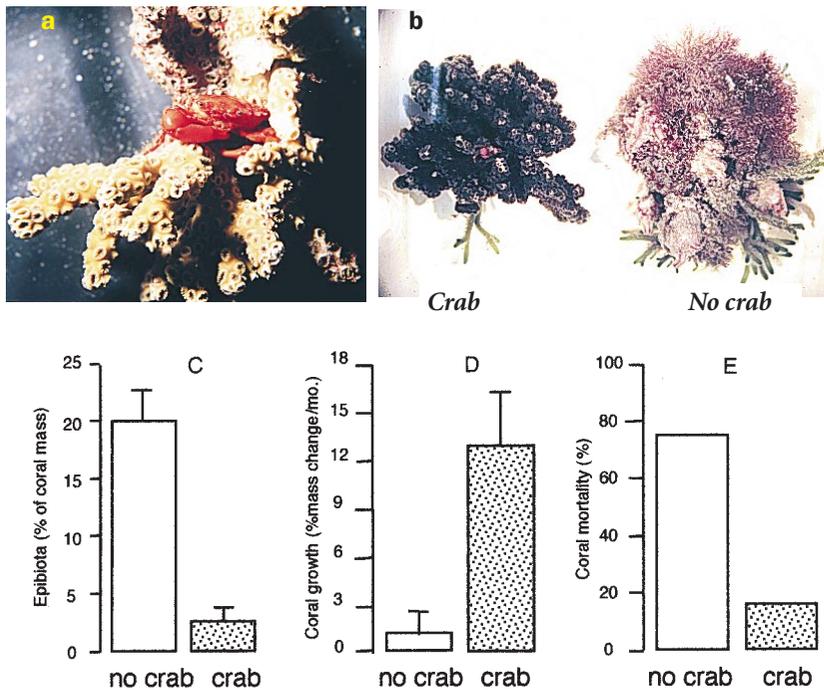


Figure 4. Mutualism and refuge from competition for a foundation species. (a) The crab *Mithrax* forces hiding within the branches of the coral *Oculina arbuscula*. The interaction between the two is mutualistic in shallow, well-lit waters where corals are at a competitive disadvantage vis-à-vis seaweeds and sessile invertebrates and the crabs are highly susceptible to predation by fishes. (b) When corals are grown in the field without crabs, they are smothered by a dense covering of seaweeds and invertebrates. By reducing overgrowth (c), the crab increases coral growth (d) and survival (e), enhancing the production and maintenance of the biogenic structure formed by this branching coral and indirectly facilitating a community of over 300 species of invertebrates and several fishes. The crab directly benefits from the interaction in two ways: It gains a refuge from its predators and the coral provides the crab with nutritional supplements. Figures modified from Stachowicz and Hay (1999a). Photos by J. J. S.

interactions that facilitate the growth and survival of these organisms clearly play an important role in structuring ecological communities.

All the interactions mentioned above can be (although are not necessarily always) mutually beneficial. The associates receive protection from their predators (Witman 1987, Stachowicz and Hay 1996, 1999a) or nutritional rewards (Janzen 1966, Glynn 1976, Stachowicz and Hay 1999a) for their services. Such positive feedback between the associate (crabs, urchins, ants) and the foundation species (corals, mussels, trees, respectively) may ultimately stabilize the overall community.

Plants and sessile animals can also reduce competitive stress indirectly by living with or near parasites or competitors of the species with which they compete. In coastal marshes of the western United States, a parasitic plant facilitates two relatively uncommon plant species by selectively infecting and suppressing the competitive dominant, *Salicornia virginica* (Pennings and Callaway 1996). Indirect facilitation can also

occur when one plant suppresses a species' competitors more than it suppresses the species itself, although this has not often been demonstrated. In one example from a Northern California riparian community, the sedge *Carex nudata* directly facilitates an entire plant community by providing a stable habitat, but it also competes with each species in that community for resources (Levine 1999). *Carex* has a strong negative impact on the monkey flower (*Mimulus guttatus*), which in turn competes strongly with numerous other plant species and reduces their abundance. Manipulative experiments showed that by reducing competition from the monkey flower, *Carex* indirectly benefited the liverwort *Conocephalum conicum* more than it harmed the liverwort through direct competition (Levine 1999). Competition can be alleviated by a host of indirect mechanisms, but simultaneous assessment of the direct and indirect costs and benefits are needed to obtain an accurate picture of the net outcome of a species interaction (Miller 1994).

Multiple stresses. Most, if not all, investigations of positive interactions have focused on how a single stress is alleviated and on how the outcome of an interaction changes with variation in that particular stress. But different stresses limit a species at each extreme of its distribution. For example, physical stress usually determines the upper elevational limit of a species (up the side of a mountain or in the intertidal zone), while the lower elevational limit is determined by

the stress of competition or predation, which intensifies as physical stress diminishes. There seems no reason why different positive interactions could not operate to ameliorate each of these stresses (physical stress and competition) and extend the species distribution vertically in both directions, although to my knowledge no single study has demonstrated this experimentally. Examining the role of positive interactions over the entire range of conditions in which a species occurs would help expand our understanding of the scale and extent of their influence. Marine intertidal and terrestrial montane communities might prove particularly useful for addressing these questions because the relatively compact nature of their stress gradients allows simultaneous experimentation at both borders of a species' distribution.

As one example, I have shown that two different positive interactions extend the upper and lower limits to the vertical distribution of a New England rocky shore seaweed. The red alga *Chondrus crispus* occurs higher into the intertidal zone beneath a canopy-forming seaweed (*Fucus*) than it does when

that canopy is removed, because temperatures and desiccation stresses are lower beneath the *Fucus* canopy. The same red alga can occur deeper into the subtidal zone when it is inhabited by small gastropods that consume competitively superior invertebrates that can encrust and smother algal fronds. Given the many types of stresses that positive interactions appear to be capable of ameliorating, I suspect that most species will be involved in different positive interactions at each edge of their distribution.

Positive interactions and species diversity

Given recent evidence that more diverse communities may have enhanced ecosystem function with respect to processes such as carbon fixation, stability, and resistance to invasion (Chapin et al. 1998), the impacts of positive interactions on local species diversity are worthy of consideration. Because many of the positive interactions discussed here involve the provision of biogenic habitat, the impacts of these interactions on diversity should be obvious: Entire communities disappear without the one keystone facilitator or foundation species (Dayton 1975, Jones et al. 1997). In this respect, these interactions are no different than other forms of

interaction such as predation: For example, that keystone predators can enhance community diversity by suppressing competitively dominant species is widely appreciated (Paine 1966). Indeed, the importance of positive indirect effects on species diversity via keystone species effects and trophic cascades have been well documented: The urchin–mussel (Witman 1987) and crab–coral (Stachowicz and Hay 1999a) mutualisms discussed in “Refuge from competition” are two examples.

Ecological theory suggests that dominance of a community by one or a few species leads to the exclusion of other species from the community in the absence of disturbances that remove the dominant species (Paine 1966, Sousa 1979). Under these models, diversity is predicted to be greatest at intermediate levels of stress or disturbance, because at low disturbance (or stress or predation) levels, communities are monopolized by a competitive dominant, and where stresses are intense, only a few species are tolerant enough to persist (Figure 5, solid curve). However, this pattern may not occur in communities where competition affects growth but not mortality (Peterson 1991). For example, in a subtidal algal community, as dominance by the unpalatable brown seaweeds *Sargassum* and *Padina* increases, total seaweed species richness

also increases because *Sargassum* and *Padina* provide refuges from herbivory for palatable red and green seaweeds (Hay 1986). Competition with brown algae does reduce the growth rates of red and green algae, but where herbivory is intense, survival is enhanced relative to plants grown in the absence of brown algae. Thus, where associational defenses are common, classical ecological theories of diversity may not be adequate to explain patterns observed in nature.

Hacker and Gaines (1997) have modified the intermediate disturbance hypothesis to account for the effects of such positive interactions on species diversity. Positive interactions enhance species diversity where predation is intense by providing a structural or chemical associational refuge (Figure 5, dashed curve; Hay 1986). However, positive interactions may do more than broaden the conditions under which higher diversity is maintained; they may actually increase the maximum observed diversity of a community. Hacker and Gaines (1997) point out that the well-documented increase in species diversity at intermediate stress levels need not be solely a direct consequence of the alleviation of competition. As disturbance or predation increases, facilitators may be released from competition, further enhancing diversity due to facilitation (Figure 5, dotted curve). In a recent test of this prediction, Hacker and Bertness (1999) showed that the absence of

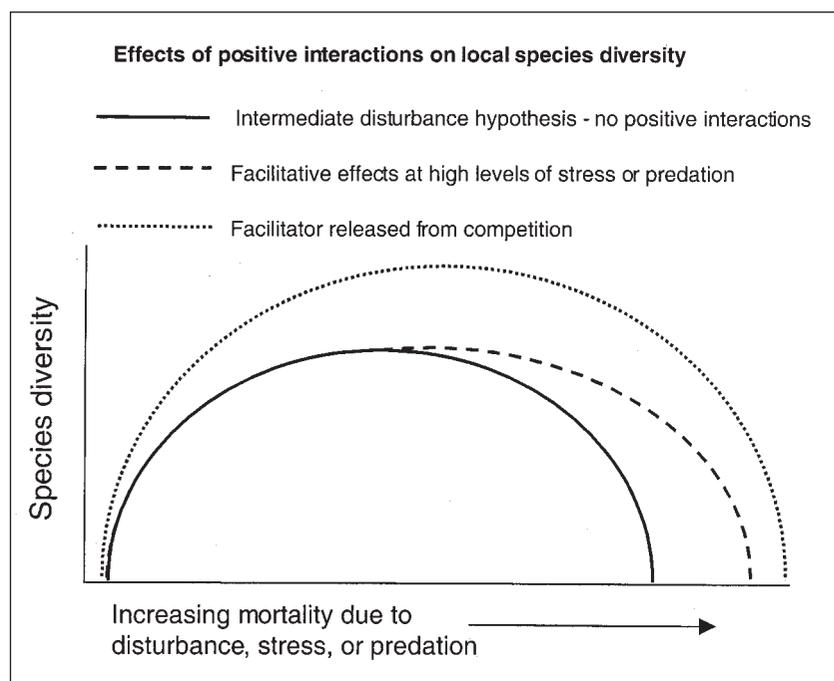


Figure 5. Conceptual model of the impact of positive interaction on local species diversity. The solid line represents the conventional view of the maintenance of high species diversity via intermediate levels of physical or biotic disturbance preventing competitive exclusion (e.g., Sousa 1979). The dashed line depicts increases in the level of disturbance (stress) at which high diversity can occur thanks to the habitat-modifying effects of positive interactions. The dotted line depicts a facilitator allowing high diversity in more stressful conditions (as in the dashed line) and also increasing the maximum observed diversity because the facilitator species is released from competition at increasing levels of stress or disturbance. Redrawn from Hacker and Gaines (1997).

a competitive dominant and intermediate levels of physical stress in marsh communities are necessary, but not sufficient, for maintaining high local diversity; the presence of a habitat-modifying facilitator species is also required. Although the Hacker and Gaines model is largely untested, studies of other positive interactions discussed in this article do appear to support it. For example, on shallow-water reefs in North Carolina, as herbivory by crabs increases, corals are freed from competition with fleshy seaweeds (Figure 4); the biogenic structure produced by these corals provide habitat that facilitates numerous invertebrates not found in algal communities (McCloskey 1970, Stachowicz and Hay 1999a).

Although these examples provide tantalizing evidence of the ways that positive interactions can enhance local species diversity, it is at least possible that positive interactions could decrease local diversity if, for example, the facilitated species can exclude other species by competition or predation (Hartnett and Wilson 1999). Further detailed experimentation will be needed to assess whether positive interactions more generally enhance or decrease local species diversity. However, at sufficiently large scales, the net effect of positive interactions will undoubtedly be to enhance regional species richness via an increase in habitat diversity (Jones et al. 1997).

Variation in the outcome of interactions

The strength of the benefits of positive interactions become increasingly important to species persistence with increasing stress levels—for example, when species are located higher in the marine rocky intertidal zone (Bertness and Leonard 1997) or at higher elevations near the timberline in mountains (Callaway 1998), or during drought years (Greenlee and Callaway 1996). The stresses that generate positive interactions can also vary on geographic scales: Thermal stress and predation pressure, for example, are both thought to be more intense at lower latitudes, suggesting that there may be a corresponding latitudinal gradient in the strength and importance of positive interactions. Although there are few data available to test this hypothesis, the benefits of living with conspecifics or heterospecifics that provide refuge from thermal stress does decrease with increasing latitude, as thermal stress declines (Bertness et al. 1999, Leonard 2000). A similar latitudinal gradient in predation pressure appears to drive changes in the nature of associational defenses used by decorator crabs (Stachowicz and Hay 2000).

When stress is diminished, the benefits derived from the interaction decrease, and the net outcome of a formerly positive interaction may become neutral or even negative. Thus, there is a need to shift from a framework that treats competitive and facilitative interactions as two sides of a coin to a fundamentally different perspective that considers mutualism and competition to be part of a gradient of possible outcomes of interactions among species (Bronstein 1994b). Particularly valuable are studies that simultaneously address the costs and benefits of any interaction to both species involved and the manner in which each component changes with environmental fluctuations (e.g., Holzapfel and Mahall 1999).

Such dissections should be encouraged, as they allow for a mechanistic understanding of how environmental variation alters the magnitude of individual costs and benefits, and how these combine to produce variation in the overall outcome of an interaction in space and time. Recent theoretical and empirical advances in the measurement of interaction strength will most likely aid in these endeavors and enhance our ability to compare results among studies and systems. However, it is important to recognize that each metric has its own biases and limitations that dictate the types of conditions under which each is most appropriate (Berlow et al. 1999).

The relative balance of costs and benefits to an interaction can also shift with changes in the morphological or chemical composition of a species, which can vary geographically, temporally, and through ontogeny. The density and architectural complexity of plants or sessile animals can influence their ability to modify the physical or biotic environment and thus alter their ability to facilitate other species (Woodin 1978, Hacker and Steneck 1991, Levin and Hay 1996). Similarly, intraspecific variability in host-plant chemistry could result in dramatic changes in the refuge value of some plants (Hare 1992). Even if the critical characteristics of facilitator species remain relatively constant over time, the utility of the refuge to individuals of other species may change through their ontogeny. For example, although seedlings of many species benefit from associating with adults of other species for the various reasons discussed above, this benefit typically diminishes as the seedlings become more hardy and resistant to physical stress, competition, or predation (Callaway and Walker 1997). Relatively few studies have directly explored changes in the outcome of pairwise positive interactions through ontogeny.

The dependence of habitat-modifying ability on these various correlates of size and age begs the question of how it is that many mutualistic interactions become established in the first place. For example, when habitat-forming organisms like trees or corals depend on the mobile species that they harbor for protection from their own predators or competitors (Janzen 1966, Glynn 1976, Witman 1987, Stachowicz and Hay 1996, 1999a), an interesting “chicken-and-egg” problem arises: How do juvenile corals or tree seedlings become established and grow to a sufficient size to harbor mutualists that can deter predators or competitors? Temporal refuges due to seasonal reprieves in the relevant physical or biotic stresses may be enough to allow some species to make it through the establishment phase, but this outcome seems unlikely for many slow-growing, long-lived foundation species. Perhaps rare events such as unusually high recruitment or infrequent large-scale disturbance play an as yet unappreciated role in the establishment of these mutualisms and in the shift between alternative community states (see Petraitis and Latham 1999 for a recent discussion). For most communities, our knowledge of the establishment phase lags far behind that of how these interactions function and are maintained once they are established.

Conclusions

In the past two decades, ecologists' view of positive interactions has gradually shifted from one that considered these interactions to be natural history curiosities to one that recognizes that they are at least as important as negative interactions and physical forces in determining the distribution and abundance of species. Many smaller-scale positive and negative interactions that are many ecologists' focus of study are nested within, and dependent upon, larger-scale positive interactions that create the habitat within which these interactions occur (Jones et al. 1997, Bruno and Bertness 2000). When smaller-scale interactions create positive feedback that benefits habitat-modifying organisms—that is, when a mutualism exists between habitat modifiers and other species—community stability may be enhanced. This hypothesis has rarely been tested in field experiments, and the interplay between small-scale and large-scale positive interactions represents an exciting challenge for future studies.

A major advance in the study of positive interactions came from the realization that, like other forms of species interactions, the outcome of these interactions is dependent on environmental conditions. The same pair of species can be mutualists, commensals, or even parasites (Bronstein 1994b)—the “positive” interaction is just one end of a continuum of possible outcomes. Our current challenge is to develop an understanding of how variability in environmental conditions, as well as key morphological and chemical characteristics of the participants, causes shifts along this continuum. The realization that environmental conditions matter is particularly timely in light of scenarios of global climate change that predict increased temperatures. Indeed, the importance of habitat-ameliorating positive interactions will very likely grow as global environmental stress increases.

The loss of biodiversity may be the single biggest threat faced by the world's ecosystems. Much of this decline can be attributed to destruction of critical habitat such as tropical rain forests and coral reefs—critical habitats in many cases provided by foundation species through habitat-ameliorating positive interactions. On large spatial scales, positive interactions undoubtedly increase species diversity by increasing the numbers and types of habitats available for colonization. However, the impacts of positive interactions on local-scale diversity has been studied in only a few cases. Further research is needed to clarify whether these impacts can be predicted with the use of current models. Regardless, it is clear that simply preserving facilitators or mutualists in marine reserves or national parks will probably fail to stem the tide of declining biodiversity, because the effectiveness of facilitators depends on their size, density, morphology, and chemistry, all of which vary with local biotic and abiotic conditions (Woodin 1978, Hare 1992, Levin and Hay 1996, Bruno and Bertness 2000). Without a thorough understanding of the mechanisms and conditionalities underlying positive interactions, it is unlikely that we will be able to develop effective strategies for

ecosystem management to meet the challenges posed by global change.

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