

Inclusion of facilitation into ecological theory

John F. Bruno¹, John J. Stachowicz² and Mark D. Bertness³

¹Department of Marine Sciences, The University of North Carolina at Chapel Hill, Chapel Hill, NC 27599-3300, USA

²Section of Evolution and Ecology, The University of California at Davis, Davis, CA 95616, USA

³Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA

Investigations of the role of competition, predation and abiotic stress in shaping natural communities were a staple for previous generations of ecologists and are still popular themes. However, more recent experimental research has uncovered the largely unanticipated, yet striking influence of facilitation (i.e. positive species interactions) on the organization of terrestrial and aquatic communities. Modern ecological concepts and theories were well established a decade before the current renaissance of interest in facilitation began, and thus do not consider the importance of a wide variety of facilitative interactions. It is time to bring ecological theory up to date by including facilitation. This process will not be painless because it will fundamentally change many basic predictions and will challenge some of our most cherished paradigms. But, ultimately, revising ecological theory will lead to a more accurate and inclusive understanding of natural communities.

The view of a natural world structured by conflict and privation dominates ecology and has been supported by nearly every influential ecologist since Darwin. Notable examples include the mathematical models of interspecific competition developed by Lotka and Volterra, Gause's competitive exclusion principle, and both Hutchinson's and MacArthur's work on the niche and species packing. The influence of these and other related ideas on ecology was enormous, because they set both theoretical and empirical ecology on a course with little digression for over 50 years. During this period, most ecologists worked on the importance of competition, predation, physical disturbances and physiological stress in structuring communities [1]. However, more recent research clearly indicates that the influence of facilitation (Box 1) on population- and community-level variables is at least as important as other factors. Experimental investigations from a wide variety of habitats have demonstrated the strong effect of facilitation on individual fitness, population distributions and growth rates, species composition and diversity, and even landscape-scale community dynamics (see references in [1–6]). Some of the first natural historians, including Aristotle, were aware of mutualisms. The view that facilitation is an important community-level process is certainly not new [1], but the perceived importance of facilitation waned

during the development of modern ecological theory [1,2]. As a result, current theory considers only the negative interactions and abiotic factors that deplete populations and remove species, and largely ignores the credit column of the ecological ledger. Our purpose here is to begin to amend this oversight. We consider how inclusion of facilitation into the theory, models and paradigms of population and community ecology can alter many basic predictions, and argue that this is crucial to our understanding and conservation of natural communities.

Facilitation and the niche

Including facilitation in the niche concept can alter the relationship between the fundamental and realized niche as well as predictions of where a species can and will live in the physical world. Because the niche is a core principle, these changes cascade through the theoretical landscape of ecology. Originally defined by Grinnell [7] and Elton [8], the idea was refined in 1957 by Hutchinson [9] when he distinguished the fundamental from the realized niche. As defined in current ecology textbooks [10–13], the fundamental niche is the range of environmental conditions within which a species can live indefinitely in the absence of negative interspecific interactions (i.e. competition, predation and parasitism). The realized niche is sometimes formally considered to be the realized resource utilization within the conceptual niche space, but is more commonly (and practically) viewed as the restricted physical space actually occupied by a species after exclusion by competitors and others enemies [10–13]. Hutchinson himself was pragmatic about the niche concept and argued that the points of the fundamental niche could be mapped onto physical space, thus predicting where a species should be able to live [9].

The niche concept implicitly assumes that neighboring species have negative impacts (or a niche-shrinking affect) on one another [14] and is firmly bound to the notion or 'principle' of competitive exclusion (that no two species can occupy the same niche). Incorporating facilitation into niche theory leads to the paradox that the spatial extent of the realized niche of a species can be larger than the spatial range predicted by the fundamental niche (Fig. 1a) [14]. For example, on rocky shores, intertidal seaweed canopies reduce thermal and desiccation stresses, and can extend the distribution of many organisms to higher tidal heights than they are normally capable of occupying

Corresponding author: John F. Bruno (jbruno@unc.edu).

Box 1. What is facilitation?

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 can occur when one organism makes the local environment more favorable for another either directly (such as by reducing thermal, water or nutrient stress via shading or through nutritional symbioses), or indirectly (such as by removing competitors or deterring predators). Facilitations include tightly coevolved, mutually obligate relationships as well as much looser, facultative interactions. Facilitations are ubiquitous: they 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. Many species modify the local environment and facilitate neighboring species simply through their presence. Trees cast shade on the forest floor, altering light and moisture regimes, and corals form reefs, increasing habitat complexity and thereby providing habitat for countless other species. Other more intimate facilitations include pollinators and seed dispersers, which are crucial to the reproduction

and dispersal of many plant species. Some mutualisms involve the physical intermingling of two species throughout much of their life history: lichens are associations between algae and fungi; corals are associations between a cnidarian and a dinoflagellate; many terrestrial plants have symbiotic bacteria or fungi that enhance nutrient or water uptake. Refer to recent reviews on the ecology of facilitation and mutualism for further examples [a–d].

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[15]. Substrate stabilization by the intertidal grass *Spartina alterniflora* on New England cobble beaches expands the landscape-scale range of a whole community of plants and invertebrates [16,17]. Similarly, the mutualisms between corals and symbiotic dinoflagellates [18] and between mycorrhizal fungi and vascular plants [19] enable corals and plants to persist across a broader range of physical conditions than would be possible in the

absence of these mutualists. Likewise, the modification of soil conditions by early successional plants and trees after glacial retreats facilitates the subsequent range extension of countless associated species [20]. In all of these cases, the niche or physical space occupied by a species in the presence of interspecific interactions is actually greater than that occupied when the species lives alone.

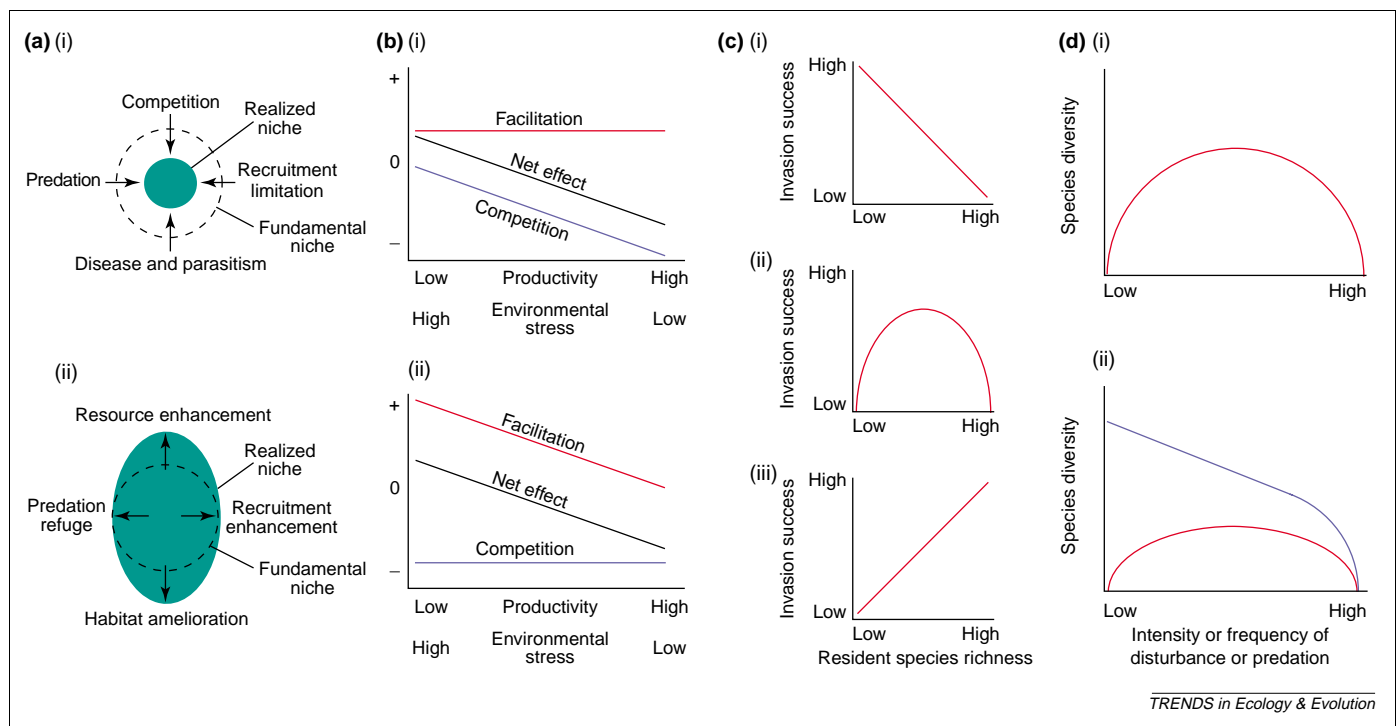


Fig. 1. Four fundamental models of ecology, with and without facilitation. (a) When facilitation is considered, the realized niche (green circle) can be larger than the spatial range predicted by the fundamental niche (dashed line) (ai). Incorporating facilitation into the niche concept (a(ii)) recognizes processes that can expand the amount of space that meets the requirements of the fundamental niche and can mitigate the effects of niche-shrinking factors. (b) Species interactions often comprise both competitive and facilitative components. This complicates measurements of competition because most experiments only measure the net interaction strength and assume that the strength of facilitation is minimal or constant. However, changes in the net effect across an environmental gradient can be driven by variation in either interaction component [(b(i)) facilitation weak, constant; (b(ii)) facilitation strong, variable]. (c) The relationship between diversity and invasion success becomes unimodal (c(i)) or positive (c(ii)) when the role of facilitation in enhancing both colonization and postcolonization survival is considered. (d) The current view of 'community dominants' does not always consider their impact as whole-community facilitators that generate habitat and dramatically increase species diversity (d(i)). When facilitation is considered (d(ii)), the predictions of the intermediate disturbance hypothesis are different for primary (red line) and secondary (blue line) space holders. Small organisms, in particular, often depend on habitat complexity, which can be greatest when habitat-forming species dominate and the frequency or intensity of disturbance or predation is low.

Species interactions can also reduce or eliminate the effects of niche-shrinking factors, thereby increasing the proportion of the fundamental niche that is ultimately occupied. For example, plant densities and distributions can be increased by both plant and animal facilitators that reduce herbivory [21–24]. Such facilitations enable a species to exploit a greater portion of available resources (e.g. space, light, nutrients, food, etc.) and thus increase the utilization of the fundamental niche space. Animal-facilitated dispersal of fruits and seeds can increase plant distributions [25], which minimizes dispersal limitation, an important reason why many species occupy only a small proportion of their fundamental niche. This is just a brief list of many potential examples from a variety of systems. Incorporating facilitation into niche theory, or at least acknowledging that the contemporary niche concept does not recognize this ubiquitous class of species interactions is clearly long overdue.

Positive density dependence at high population densities

A negative relationship between population density and individual fitness is a cornerstone of population biology. However, one of the most important and overlooked results of recent field investigations of facilitation is that survivorship can be positively related to population density. It is widely appreciated that positive density dependence can occur at low densities via the Allee effect, which can increase fertilization rates and propagule survival. But recent work has highlighted the benefits of living in high-density aggregations. In high rocky intertidal habitats in southern New England, the reproduction, survivorship and growth of sessile invertebrates and macroalgae are greater for higher than for medium densities [3,26,27]. Experimental thinning reduces these fitness parameters, because at high densities, neighbors buffer each other from potentially lethal thermal stress [26]. Evidently, there are often both costs and benefits to living in high and low population densities, the net balance of which is driven at least partially by the degree of ambient environmental stress [28,29]. Several studies indicate that group benefits overwhelm the costs of crowding in the stressful, high intertidal zone, but do not operate in the cooler, low intertidal, where high densities often result in very high juvenile and adult mortality [26]. Additionally, recent experimental field studies indicate that this switch from net positive to net negative effects of high density also occur across larger spatial stress gradients (e.g. from sheltered bays to exposed coasts and across regions [27]). Evidence of the benefits of high population densities is by no means restricted to marine environments. It is well established that in harsh terrestrial environments, such as deserts and alpine communities, high seedling and adult plant densities can increase growth and survivorship [2,22,24].

How can such results be reconciled with the traditional emphasis placed on negative density dependence? Populations that experience positive density effects at one life stage (e.g. adult survival and reproduction) might experience negative density dependence at another stage (e.g. recruitment). Temporal fluctuations in environmental conditions could also result in frequent switches between positive and negative density dependence within a single

life-history stage. Traditionally emphasized negative density-dependent factors (e.g. competition, disease and recruitment) are certainly important, but our predictive power hinges on a full consideration of both the positive and negative effects of density and how each of these varies across gradients of biotic and abiotic conditions.

Interaction strength models: incorporating interaction components

Several prominent ecological models make predictions about how the negative effects of predators or the strength of competition vary across environmental gradients of stress or resource availability. Such environmental stress models can be modified to incorporate positive interactions (Box 2), sometimes with surprising results. However, species interactions often comprise both negative (competitive) and positive (facilitative) components [29]. For example, in deserts, shrubs or ‘nurse plants’ facilitate the germination of seedlings of herbaceous plants by reducing soil temperature and increasing water content [30], but negatively affect seedling growth by reducing light. The compound nature of species interactions complicates empirical tests of environmental stress models because most experiments only measure the net interaction strength. If the strength of competition varies across the gradient of interest and the strength of facilitation is constant, measures of the net interaction strength will be equivalent to the competitive component (Fig. 1b) [31]. But an equally realistic scenario in which the strength of facilitation decreases with environmental stress [28] and competition remains constant will produce an identical change in net interaction strength (Fig. 1b).

There will certainly be cases in which a measurement of the net effect will be sufficient. But true tests of most mechanistic ecological models based on the context dependency of species interactions require measurements of both interaction components. These components can be separated experimentally using competition or facilitation ‘mimic’ treatments [30]. The growing recognition that species often simultaneously compete with and facilitate each other also complicates the competitive exclusion principle. If competing species also form a mutualism, then can they coexist in the same niche? Plants compete for resources such as nutrients and light, and superior plant competitors are often more susceptible to herbivore damage. These competitive dominants sometimes rely on associations with competitively inferior, but grazer-resistant neighbors to reduce herbivory [22,23]. Thus if the superior competitor begins to exclude the weaker species, it becomes more susceptible to herbivores and a negative feedback allows both species to persist [23]. As Gause and Witt demonstrated in 1935 [32], changing the Lotka–Volterra competition model into a mutualism model by switching the sign of the interaction coefficients predicts that mutualisms can result in a stable equilibrium, where the densities of both species can be greater when they co-occur [1].

Relationship between species diversity and community invasibility

The hypothesis that resident diversity is inversely related to the susceptibility of communities to invasion is an

Box 2. Incorporating facilitation into environmental stress models

Environmental stress models make predictions about how the relative importance of factors that affect the density of a prey or 'basal' species (e.g. competition and predation) vary across a gradient of environmental stress. Some environmental stress models assume that predators are more susceptible to abiotic stress than are their prey and are called 'predator stress models'. Incorporating facilitation into predator stress models, such as the original Menge–Sutherland model [a] (Fig. 1a) substantially changes many predictions. For example, intra- (Fig. 1b) or interspecific (Fig. 1c) facilitation will increase population densities at medium-high to high levels of stress. However, it is possible that an interspecific facilitator (Fig. 1c) might also facilitate predators, which would in turn reduce prey densities [b,c]. Amelioration of environmental stress remains important, but it now increases predation intensity and has an indirect negative effect on the prey. At the highest stress level, facilitation will no longer effectively ameliorate the environment. Prey densities will decline, but at a much higher level of environmental stress relative to the Menge–Sutherland model without facilitation (Fig. 1a versus Fig. 1b). Somewhat paradoxically, the inclusion of facilitation also increases the importance of competition at high and low extremes of environmental stress. This is because facilitation is expected to increase prey densities in these ranges. When environmental stress is low and predators are abundant and unrestricted, associational defenses are expected to reduce the intensity and importance of predation, resulting in increased prey densities (Fig. 1b).

However, the balance between the importance of predation and associational defenses is not entirely straightforward and making a realistic prediction requires a basic understanding of the natural history of the interaction. If the predation refuge is absolute, predators will rarely be able to consume the prey, although they might still affect densities or individual fitness (e.g. by affecting prey foraging behavior). If the refuge only reduces predator foraging efficiencies, predation and associational defenses might be equally important at medium to low levels of stress.

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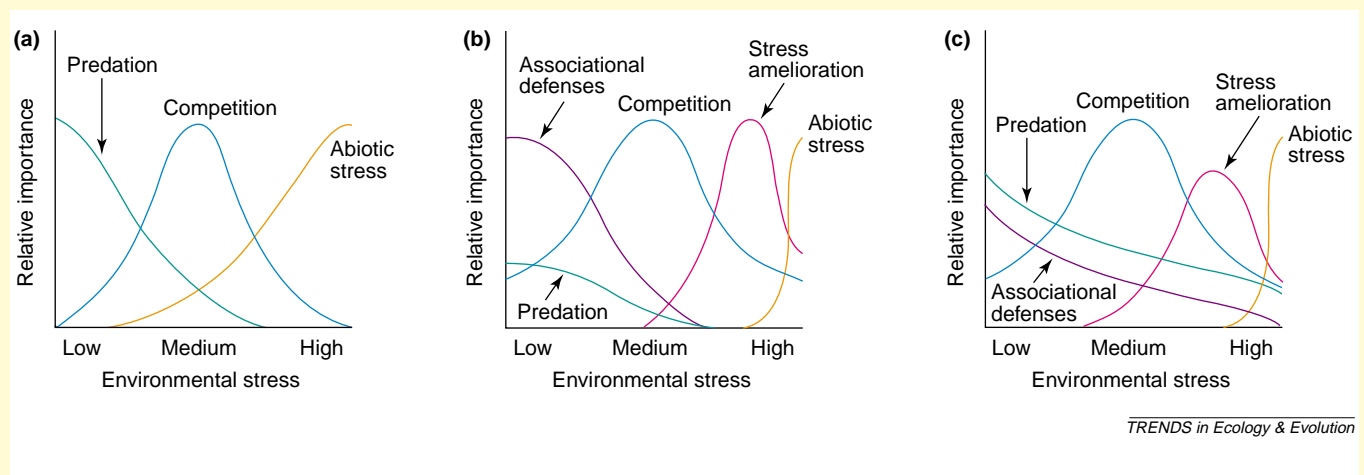


Fig. 1. The Menge–Sutherland model without and with facilitation. Models predict the relative importance of predation, competition, abiotic stress and two types of facilitation (amelioration of abiotic stress and associational defenses). All models assume high levels of recruitment of the basal (prey) taxa. (a) original model; (b) inclusion of intraspecific facilitation; and (c) inclusion of interspecific facilitation. Reproduced, with permission, from [d].

important manifestation of the primacy of biotic resistance in our thinking about what drives colonization and invasion success (Fig. 1c). The implicit assumption is that competition is a primary force controlling community composition; therefore, diverse assemblages should use resources more fully and leave little niche space for potential colonists [33]. Recent experimental and observational studies indicate that diversity can reduce invasion success in the field [34,35], at least when most other potentially important factors are removed or held constant. However, competition can be overwhelmed by other processes [36], and the benefits of increasing diversity could also be due to facilitative interactions among natives, potentially because increasing facilitator or mutualist diversity enhances invasion resistance. Additionally, habitat-ameliorating positive interactions can result in a positive relationship between species diversity and

community properties (e.g. biomass, space occupancy, productivity and disturbance resistance) [37] that could increase or decrease the susceptibility of a community to invasion [35].

Positive interactions could also change the fundamental shape of the relationship between diversity and invasibility. In many communities, foundation species (*sensu* [5,38]) provide habitat for other species and, in their absence, the overall diversity of both native and non-native species often declines [5]. Current evidence in support of a negative diversity–invasibility relationship comes from relatively small-scale experiments (e.g. [34–36]) that implicitly or explicitly ignore habitat-modifying positive interactions that occur at larger spatial scales and that might be crucial for invasion success. Communities with more species have a greater probability of containing one of these key facilitator species (i.e. the

sampling effect *sensu* [39]). However, once key habitat-forming species are present, further increases in the number of species could decrease the likelihood of invasion resulting in a unimodal relationship between species diversity and invasion success (Fig. 1c). The precise shape of the curve (symmetrical versus skewed left or right) depends on the level of richness at which: (1) foundation species or other key facilitators enter the community; and (2) competition becomes intense enough to reduce colonization.

Finally, in particularly stressful environments where habitat amelioration is an important structuring force [28], resident species could facilitate rather than compete with colonizers. Taken to an extreme, this leads to the prediction that resident diversity can be positively related to invasibility (Fig. 1c). Two recent reviews [40,41] outline a surprising number of cases in which exotic plants and animals are dependent on facilitation by resident species. For instance, many exotic plants are pollinated and dispersed by native birds and mammals and are facilitated by native plants and mycorrhizal fungi [41]. That facilitative inclusion can outweigh the effects of competitive exclusion fundamentally alters our perspective on the causes and effects of exotic invasions [41], and we can no longer assume that natives can exclude exotics or that exotics will eventually displace natives.

The inclusion of facilitation into the diversity–invasibility paradigm highlights the hierarchical organization of natural communities, which are initially dependent upon habitat provision by foundation species, with negative interactions nested within, and dependent upon, this framework [5]. This has broad implications for community assembly and island biogeography because it indicates a nonrandom colonization sequence driven by facilitative succession (one of the few modern concepts that includes facilitation). This occurs when, for example, certain species that provide habitat, such as trees or shrubs, must become established before successful colonization by understorey plants, birds, or other animals [2,24]. Colonization rates will also be affected by facilitation where arrival or retention of propagules is enhanced by the presence of a facilitator [2,25,42,43]. For many species, small oceanic islands (or small patches of fragmented forest) are likely to be more environmentally stressful than are larger islands because of their greater perimeter:area ratio. Given that facilitative interactions appear to be more common in harsh environments [15,28,29], we might expect facilitation to be more important in smaller or more isolated islands. Interestingly, MacArthur and Wilson [44] recognized the potential role of facilitation in colonization in their initial treatise on island biogeography, but did not formally consider the implications of facilitation on their theory. Certainly, facilitation is now known to be sufficiently common that it should be explicitly incorporated into our thinking about recolonization and invasion dynamics.

Do competitive dominants enhance or diminish local diversity?

In the current view, many foundation species are considered ‘competitive dominants’ that can exclude

other potential primary space holders [45–47]. However, by providing habitat for numerous smaller species, their net effect on species diversity can actually be positive. This realization has important implications for the predictive ability of theories based on exclusion by a ‘competitive dominant’, such as the keystone predator [45,48] and intermediate disturbance hypotheses [49]. For example, as originally demonstrated by Paine [45,48], intertidal mussels can displace other large sessile species (e.g. seaweed and barnacles), reducing the diversity of primary space holders. However, mussel beds provide habitat for a large number of associated invertebrate species [50–52]. Many more species are associated with mussel beds than with other primary space holders [53], hence, total species diversity is higher when mussels are present [50–54].

That keystone species can decrease community-wide diversity by removing habitat-forming competitive dominants is well known in other systems where the species are larger or economically important, and thus more apparent to humans. For example, although sea urchins dramatically reduce giant kelp biomass, releasing other seaweeds from competition, the removal of kelp forests by sea urchins results in a dramatic decrease in community diversity [55]. There are many other similar examples, such as overgrazing by rodents, ungulates or other terrestrial herbivores, that can prevent the development of plant communities and reduce overall species diversity. In all of these cases, the effect of keystone species that consume foundation species is to increase diversity at the primary space-holder level, but to decrease diversity at the community-wide level by reducing habitat complexity. Thus, the effects of keystone species on diversity are dependent on the scale of organisms being considered. There is a similar scale dependence of the predictions of the intermediate disturbance hypothesis [56]. Sousa’s [49] experiments on intertidal boulders are frequently cited as evidence that diversity is greatest at intermediate levels of disturbance. But the diversity of invertebrates living within (and presumably being facilitated by) the macroalgae studied by Sousa is actually slightly greater at low disturbance than at intermediate disturbance [57]. In general, the diversity of secondary space holders (including both sessile and mobile associated species), as well as overall community diversity, is often highest at low levels of disturbance, where habitat complexity is greatest (Fig. 1d). Additionally, for taxa that are small relative to the habitat-forming species, diversity often increases over the course of succession and does not reach a maximum in mid-successional communities [58,59]. This suggests competitive exclusion might be weak or nonexistent for secondary space holders, and that the importance of competition should be reconsidered in these systems.

Given the limited resources available for biological conservation, it is tempting to focus management efforts on keystone species [60]. However, in addition to the logistical difficulties associated with identifying them [61], the deliberate protection or augmentation of keystone species populations might actually decrease total community diversity by reducing the abundance of the dominant habitat-forming species. The protection of keystone species is not a magic bullet for habitat

Box 3. Conservation biology and the role of foundation species

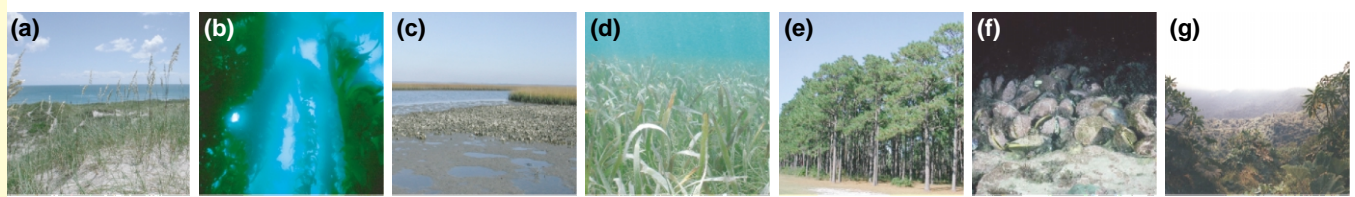
Restoring damaged habitats, conserving and managing natural resources, and predicting the future effects of current human activities are all primary goals of contemporary ecology that pose a formidable test of how well we understand natural communities. An appreciation and a thorough understanding of the importance of facilitation, especially the role of foundation species, are necessary to achieve these goals. Most natural communities are characterized by, and dependent on a single or a functional group of habitat-forming foundation species that provide the framework for the entire community [a]. Forests, temperate grasslands, marine seagrass beds and coral reefs are just a few examples (Fig. 1).

Habitat conservation efforts must focus on preserving foundation species and their role in facilitating associated species. In many habitats, this function is highly dependent on characteristics of the foundation species (i.e. their size, density, complexity, etc.) [a]. For example, the degree to which seagrass beds modify flow and sediment characteristics, reduce predation intensity and facilitate other species is, to a large degree, controlled by the height, density and flexibility of the grass blades [a,b]. This lesson is especially important for restoration ecologists, because reestablishing the role of foundation species and other important facilitators is key to restoring the characteristics and functions of the original system. Wetland restoration projects have failed when salt marshes were constructed on coarse, nutrient-poor soil, which limits the height of

habitat-generating cordgrass [c]. This in turn reduced overall habitat quality and some species, including the endangered clapper rail *Rallus longirostris*, were not able to colonize the restored marshes. Likewise, the height of restored oyster reefs in coastal estuaries significantly affects the growth and survival of the oysters and the abundance and diversity of associated fish and invertebrates [d]. Reefs that are too short or deep are subjected to potentially lethal hypoxia events.

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Fig. 1. Examples of habitats generated by foundation species that are threatened by development, pollution or overexploitation. (a) Sand dune plant community, (b) kelp forest, (c) oyster reef, (d) seagrass bed, (e) pine forest, (f) subtidal mussel bed and (g) tropical rain forest. Photographs reproduced with permission from J. Bruno (a,c–e), E. Sala (b), J. Witman (f) and J. Stachowicz (g).

conservation and is no substitute for the much more difficult task of explicitly protecting the habitat and the organisms that create it (Box 3).

Conclusion

The theoretical framework of modern ecology has not kept pace with advances resulting from experimental field research, and should be updated by the inclusion of facilitation. This is not to say that current theory emphasizing competition or predation is wrong, but that it paints an incomplete, and in some cases misleading picture of our understanding of the structure and organization of ecological systems. We have only scratched the surface, and there are other influential ideas and theories that should be considered. For example, food-web theory would be (and to some degree has been) fundamentally altered by the realization that most species interactions are indirect and positive [62,63]. After all, although rarely recognized as such, a trophic cascade is simply an indirect facilitation. Positive interactions are incredibly diverse and have a well-documented influence on every ecosystem on Earth. We encourage ecologists to consider how facilitation modifies the ecological theory that they teach at

even introductory levels and also how it might lead them to question other paradigms of ecology.

Acknowledgements

We are grateful to many colleagues for stimulating discussions that led to this article, including Emmett Duffy, Nancy Emery, Mike Graham, Mark Hay, Jonathan Levine, Tatyana Rand and Don Strong.

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