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FACILITATION

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Facilitation includes direct or indirect interactions between biological entities (i.e., cells, individuals, species, communities, or ecosystems) that benefit at least one participant in the interaction and cause harm to none. Research on ecological facilitation has steadily increased over the past three decades and is now appreciated as a fundamental process in ecology. Facilitation also has many important implications for problems in applied ecology and conservation.

HISTORICAL CONTEXT

Understanding the processes governing species coexistence and community structure is a central goal of community ecology. Historically, most ecological research has focused on the negative effects of abiotic or biotic interactions as the primary drivers of species occurrence and the organization of ecological communities. Consequently, negative ecological interactions, such as competition and predation, contribute disproportionately to the conceptual foundation upon which most ecological theory is built. However, over the past three decades there has been a growing body of literature highlighting the important role of facilitative interactions for population- and community-level processes.

Before discussing recent conceptual advancements leading from facilitation research, it is useful to briefly reflect on the history of ecology and facilitation research. The focus of ecologists on antagonistic species interactions can be traced back even to the publication of *The Origin of Species* in 1859, in which Charles Darwin metaphorically described species as wedges. In this metaphor, ecological space (the resource pie) is divided into a series of wedges that represent species' population or range sizes (i.e., proportion of the pie occupied). The addition of a new species to the resource pie or an increase in the size of the wedge of an existing species must necessarily come at the expense of other species. Indeed, the footprint of this metaphor is imprinted on the conceptual foundations of ecology and lies at the heart of many core ecological concepts, such as the competitive exclusion principle, the niche concept, island biogeography, community assembly, and community invasibility. Interestingly, in addition to setting the stage for research on negative interactions, Darwin also laid the groundwork for studying facilitation by recognizing that reciprocally positive interactions could arise in nature as a result of organisms acting with purely selfish interests. However, his insights did not permeate ecological thought until the mid-twentieth century. Indeed, it is now widely recognized that consideration of facilitation fundamentally changes our understanding of many core ecological concepts and greatly enhances the generality and depth of ecological theory. The stage has been set for rapid development of ecological knowledge as positive interactions, negative interactions, and neutral processes are incorporated into a more sophisticated archetype for ecology.

INTRASPECIFIC FACILITATION, MUTUALISM, AND COMMENSALISM

Although ecologists traditionally invoke facilitation to describe interspecific interactions, facilitation between individuals of the same species (intraspecific facilitation) also plays a key role in driving population and community dynamics. Under some circumstances, organisms can experience positive density dependence whereby individuals living in aggregations have higher growth rates, survivorship, and reproductive output. These benefits arise via a wide variety of mechanisms ranging from the reductions in per capita risk that occur as predator consumptions rate saturate at high prey densities (e.g., dilution effects) to the buffering effects of neighbors against harsh physical stressors (e.g., in rocky intertidal zones). Positive density dependence also occurs at low densities via Allee affects where a species' population growth rate rises with increasing density via increased fertilization success and propagule survival.

Facilitative interactions among populations and species are generally categorized as mutualism or commensalism. Mutualism is a specific form of facilitation in which interactions are reciprocally positive for all participants (Fig. 1). Mutualism includes highly transient reciprocally positive interactions as well as interactions that have emerged as a result of long coevolutionary histories between participants (such as plant-pollinator and plant-disperser networks). Commensalism, in contrast, is reserved for cases of facilitation where at least one participant in an interaction is positively affected while others are neither positively nor negatively impacted. Although the literature is replete with examples of mutualisms, there is a relative scarcity of examples of commensalism in nature. Consequently, some ecologists debate the relevance of this term, arguing that species interactions are more likely asymmetrical in strength (i.e., one species exhibits a strong positive response to the other, while the other exhibits a weak positive [or negative] response to the first), rather than being truly commensal in nature.

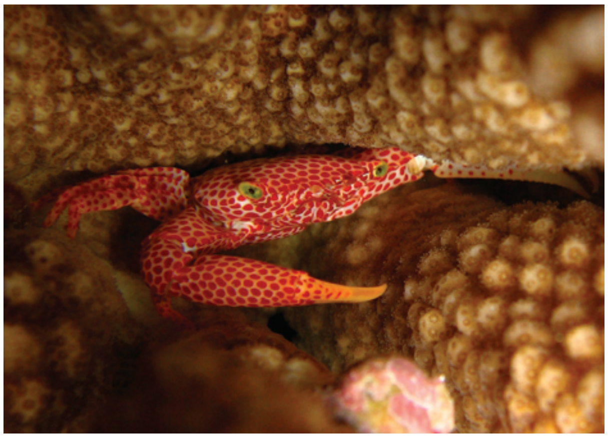

FIGURE 1 Example of mutualism. In this interaction, coral (*Pocillopora sp.*) provides habitat, shelter, and foods for crabs (*Trapezia rufopunctata.*), which, in turn, provide the coral protection by repelling coral predators. Photograph by Adrian Stier.

THEORETICAL PERSPECTIVES

While there has been much recent interest in facilitation, there is still much to learn about how positive interactions influence population and community dynamics. Theoretical developments on positive interactions have only recently begun to move beyond phenomenological descriptions to identify general mechanisms that drive ecological dynamics. Indeed, a number of recent advancements have illustrated the essential role of positive interactions for key ecological phenomena such as ecological community assembly, determining the geographical distributions of species, maintaining species coexistence, and influencing the diversity and stability of ecological communities.

Simple two-species models have most commonly been used to investigate the effects of positive interactions on species coexistence and to examine the environmental conditions where positive interactions are expected. For example, as early as 1935, Gause and Witt examined two-species Lotka–Volterra models and showed that positive interactions can be destabilizing when they are strong because they create positive feedbacks between species (e.g., mutualisms) that can lead to infinite population growth. When interaction strengths are weak or strongly asymmetrical (e.g., commensalisms), however, positive interactions can have stabilizing effects, especially when they occur in conjunction with external mortality sources such as predation, disturbance, and stressful environments. Recent investigations have shown that incorporating nonlinearities via density dependence in cost–benefit functional responses (i.e., positive effects saturate with increasing population density) has a stabilizing effect in these models. In fact, mutualistic communities characterized by nonlinear functional responses have positive complexity–stability relationships that suggest positive interactions may be important drivers of community resilience as a whole.

Phenomenological models (e.g., simulations and agent-based models) have extended the findings of a large body of empirical research to generate important insight into the conditions where positive interactions are expected to play a key role in species coexistence and persistence. In general, positive interactions are important for promoting species persistence in severe environments (e.g., arctic, salt marsh, and desert ecosystems) and extending the geographic distributions of species along range boundaries. Specifically, positive interactions can expand species range limits by enabling the expansion of the realized niche into more severe environments than would be possible without positive interactions. In these cases, one species makes local environments favorable for colonization by a second species by directly or indirectly enhancing access to resources, dispersal rate, or provision of refuge from competitors, predators, or abiotic stress. Facilitative interactions, however, are often context dependent. Most interactions between species have positive and negative components, and the relative strength of positive and negative effects is often determined by the environmental context of the interaction. For example, mutualism can change to competition along a stress gradient, and so species can exist as facilitators and competitors in different zones of a landscape.

Although models examining the effects of positive interactions on the dynamics of species pairs have provided progressive insights into the conditions where facilitation promotes species coexistence, population stability, and range limits, species rarely interact and coexist in isolation of other species or habitats. Indeed, most natural communities are characterized by complex webs of interacting species that are spatially linked to other communities via dispersal or species movements. It is likely that the effects of facilitation will not be intuitive extensions of two-species models in these multispecies and multipatch assemblages.

Several recent studies have, in fact, begun to examine spatially explicit multispecies metacommunity models that include diverse interspecific interactions and environmental stress gradients. These models reveal some general expectations for the role of facilitation in community assembly and ecosystem diversity and function. For example, poor habitat quality and low spatial connectedness is expected to favor the emergence of highly stable local communities that are strongly facilitative but characterized by low diversity and low productivity. In contrast, high habitat quality and high connectedness among metacommunity patches is expected to promote local communities that are less facilitative and less stable but characterized by high diversity and productivity (Fig. 2).

EMPIRICAL PERSPECTIVES

Foundation Species and Community Facilitation

The structure and dynamics of many widely recognized ecological communities are influenced by facilitation. In fact, many communities are identified by a foundation species that provides or creates the physical structure, conditions, and boundaries of a community (e.g., kelp beds, coral reefs, hardwood forests, mangrove stands, salt marshes, phytotelmata, and so on), which directly or indirectly facilitates a diverse array of species. Though a range of interactions including faciliation, competition, and predation may occur among species in the community, the overall persistence of the community is facilitated by the foundation species. The exact mechanism by which a foundation species facilitates a community varies among habitats. In physically stressful environments, foundation species typically ameliorate environmental stress, whereas in more benign environments they more typically provide refuge from predation. By creating patches of suitable habitat, foundation species influence community structure on a landscape scale and can be important drivers for both local and regional patterns of diversity.

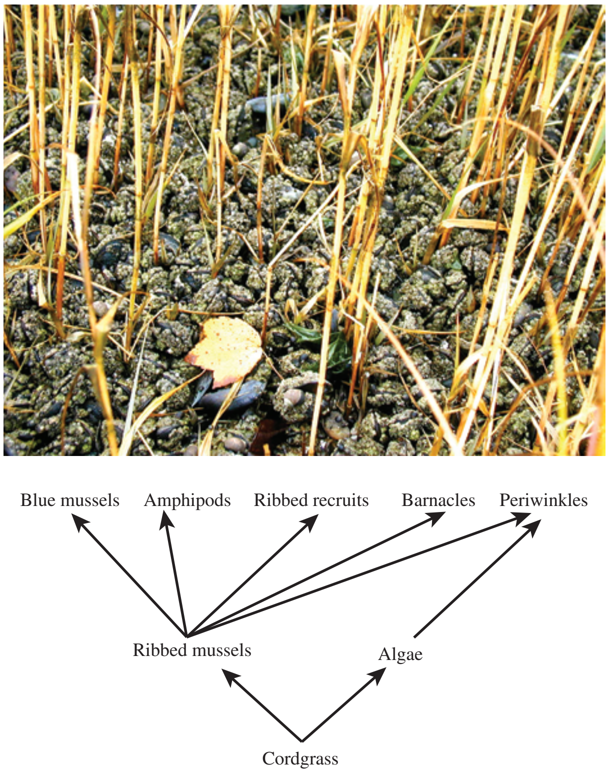

FIGURE 2 Example of a facilitation cascade in cordgrass/mussel bed communities. The establishment of cordgrass intiates a facilitation cascade whereby the establishment of ribbed mussels is facilitated by cordgrass. The synergistic effects of the cordgrass and mussels, in turn, facilitate the establishment of a variety of other taxa, including other species of mussels, barnacles, amphipods, and snails. Photograph by Andrew Altieri.

Although community facilitation is often attributed to a single foundation species, it can also be driven by the synergistic interactions between two or more species that in concert provide the foundation for communities. Facilitation of communities via synergistic interactions among foundation species has been explicitly identified in only a few habitats, such as cobble beaches and coral reefs, but could be widespread in habitats that are defined by mixtures of species, such as sea grass meadows. However, like other forms of facilitation, community facilitation is likely context dependent, with the interaction between foundation species changing from synergistic to antagonistic along an environmental gradient. At a landscape scale, this context dependency can lead to abrupt changes in species composition if foundation species exist as faciliators and competitors in different zones of the landscape.

Ecosystem Facilitation

Facilitation is also an important process operating at the highest level of ecological organization—ecosystems. Ecologists have long recognized the importance of fluxes of energy, matter, and organisms for driving ecosystem processes. When this spatial coupling benefits foundation species and their associated species assemblages in a way that increases ecosystem services (e.g., increased stability, productivity, resilience, and so on.), then the spatial coupling serves as a form of "ecosystem facilitation." Ecosystem facilitation differs from community facilitation in that it typically occurs along spatial gradients and refers to positive interactions across ecosystem boundaries, whereas community facilitation typically occurs along stress gradients and refers to species facilitation within a single community or ecosystem type. For example, in aquatic systems ecosystem facilitation occurs when plankton produced in the pelagic zone sinks and provides food and energy to support and maintain the benthic ecosystem (benthic–pelagic coupling). Ecosystem facilitation is particularly common between aquatic and terrestrial ecosystems and between productive and unproductive systems. For example, offshore seagrass beds and coral reefs can attenuate storm waves to protect intertidal mangroves and salt marshes that then provide additional energetic protection for inland terrestrial ecosystems. Mangroves and salt marshes can also reciprocally facilitate offshore sea grasses and coral reefs by catching and retaining suspended sediments and nutrients that can drive epiphytic growth and shading that is harmful to seagrass and coral ecosystems.

In these and most other examples of ecosystem facilitation, the positive interactions among ecosystems occur via provision of limiting resources (spatial subsidies of nutrients, organic matter, shelter, habitat to live in) or by reducing environmental stressors (e.g., sediments, toxins, flooding, storm disturbances, abrasion). However, spatial coupling among ecosystems is not always facilitative and can become detrimental in some contexts. For example, although plankton deposition is important for benthic ecosystems, excessive depositions may ultimately disrupt the system by choking filter feeders and stimulating bacterial blooms.

Finally, it is important to note that research on ecosystem facilitation, in contrast to population and community facilitations, is dominated by "correlative studies." Natural ecosystems are typically too large and complicated to manipulate, so the mechanistic basis of ecosystem facilitation is often difficult to identify. Thus, where manipulative experiments cannot be conducted, a weight-of-evidence approach is needed that combines rigorous site selection and data collection criteria, statistical modeling, and natural history.

CONSERVATION APPLICATIONS

Conservation biology is a goal-focused science whose primary objective is to study, protect, and preserve preidentified targets. Historically, conservation targets were specific species of concern, and conservation strategies focused on minimizing negative species and environmental interactions. Stressor-reducing approaches, however, fail to incorporate positive interactions into their designs and are being replaced by strategies that identify and harness positive interactions. Specifically, recent advancements in conservation research have instigated the expansion of conservation targets to include entire ecosystems (i.e., restoration of foundation species) and the functions and services they provide.

The common omission of positive interactions in conservation and restoration approaches has likely resulted in missed opportunities to enhance conservation projects at no increased cost, as many natural synergisms do not emerge from restoration and preservation designs focused on minimizing negative interactions. For example, when restoring coastal marshes and mangroves, traditional planting designs have been plantation style, with all plugs planted at far enough and equal distances from each other to ensure no competition. Experimental work in these systems over the past 20 years, however, has shown that mangrove and marsh plants, when growing in stressful mudflats, grow better in larger clumps and when these clumps are placed closer together. The improved growth stems from the benefits plants receive from the aeration of soils by other nearby plants. These studies also clearly show that these cooperative benefits far outweigh the negative impacts of competition for nutrients between plugs. Thus, by not updating its designs and theoretical approaches to incorporate recent findings that highlight the importance of positive interactions in the success of species under harsh physical conditions, restoration ecology is failing to take advantage of naturally occurring synergisms among species and individuals.

While this wetland restoration example is focused on the importance of incorporating positive interactions at the population level, such synergisms can also occur at the ecosystem level. For example, some approaches to protecting shoreline habitats have already begun to incorporate positive interactions among species, ecosystems, and man-made structures. The overall goal is to maximize positive interactions that surrounding or overlapping ecosystems would naturally provide each other but were lost under the old paradigm of coastal protection (remove all buffers in favor of stronger man-made structures). The combined use of hard structures to fend off flooding and erosion and wetland plant ecosystem restoration can be effective if we identify compatible and complementary aspects of engineering and vegetation adaptation measures. An excellent example comes from Dutch engineering and conservation efforts, where coastal engineers have tried to “build with nature” to increase the resilience of their man-made structures to oceanic disturbance. Levees built to prevent flooding during storms are maintained with a thick grass cover to increase their integrity. In addition, more recent efforts have focused on placing willow trees and marsh grasses just ahead of man-made levees to reduce wave action on and water levels around the protective barrier. The benefits of this type of positive-interaction engineering go well beyond natural ecosystems enhancing the integrity and efficacy of man-made structures, as the services of the planted ecosystems are not limited to this one interaction. For instance, planted marshes likely increase fishery production in surrounding areas, and willows increase carbon sequestration and habitat for local songbirds. Human utilization of the shorelines also increases, as the natural ecosystems planted on top of and around man-made structure provide recreational opportunities.

Despite advances in positive interactions and facilitation theory in ecological research over the past 20 years, the concepts have failed to make a large impact on conservation and restoration ecology. As highlighted in the examples above, incorporating positive interactions into conservation and restoration practices can occur at the organismal-, population-, community-, and ecosystem-levels and can reap substantial benefits with little additional investment in resources. Conservation and restoration plans simply need to be modified to explicitly integrate positive interactions. The old paradigm of applying terrestrial forestry and wildlife theory (i.e., minimizing competition and predation on target species) to modern-day conservation and restoration efforts needs to be updated with current ecological theory revealing that positive interactions among species under harsh conditions (i.e., those of stressed targets) are paramount to those species continued existence.

SEE ALSO THE FOLLOWING ARTICLES

Conservation Biology / Metacommunities / Resilience and Stability / Restoration Ecology / Spatial Ecology / Stress and Species Interactions / Two-Species Competition

FURTHER READING

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~~FISHERIES ECOLOGY~~

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~~Fisheries ecology is the integration of applied and fundamental ecological principles relative to fished species or affected nontarget species (e.g., bycatch). Fish ecology focuses on understanding how fish interact with their environment, but fisheries ecology extends this understanding to interactions with fishers, fishery communities, and the institutions that influence or manage fisher behaviors. Traditional fisheries science has focused on single-species stock assessments and management with the goal of understanding population dynamics and variability. But in the past few decades, scientists and managers have analyzed the effects of fisheries on target and nontarget species and on supporting habitats and food webs and have attempted to quantify ecological linkages~~