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Incorporating positive interactions in aquatic restoration and conservation

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The role of positive interactions in structuring biological communities is recognized throughout the field of ecology, but has yet to be well integrated into the restoration and conservation of aquatic systems. Here, we use examples of success in terrestrial restoration to (1) describe how a broader perspective on the scale and nature of positive interactions is necessary if we are to take full advantage of their conservation potential and (2) explain why and when positive interactions should be considered in restoration and conservation of marine, estuarine, and freshwater habitats. Such goals can be accomplished without considering positive interactions, and situations certainly exist in which positive interactions should play a minor role in restoration plans. However, a more explicit recognition of these interactions will make restoration and conservation more successful. In some cases, restoration activities may fail if these interactions are not included.

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Positive interactions are traditionally defined as interactions in which one species benefits from the presence of another species, without harm (and, potentially, with benefit) to the latter. Common examples include mutualisms (both species benefit), commensalisms (one species benefits with no measurable effect on another species), and facilitation (one species makes conditions more favorable for another species). These interactions have long been recognized as important structuring forces in natural communities (eg Clements 1916; Gleason 1927), yet only recently have they been formally included in ecological theory (Bertness and Callaway 1994; Bruno and Bertness 2001; Bruno *et al.* 2003). Experimental work over the past 15 years in rocky intertidal, salt marsh, and montane plant communities has revealed that positive relationships among species can be as important as, or even more important than competition and predation in regulating ecosystem structure and function (Bertness and Leonard 1997; Callaway and Walker 1997; Bruno *et al.* 2003; Leslie 2005), yet negative interactions (eg competition, predation) have tended to dominate ecological research over much of the past century (Bertness and Callaway 1994; Bruno and Bertness 2001; Bruno *et al.* 2005). This focus has, in turn, strongly influenced contemporary approaches to restoration and conservation.

In a nutshell:

- Facilitation is commonly used in terrestrial restoration and conservation, but positive interactions are not generally integrated into such efforts in marine, estuarine, or freshwater systems
- A broader recognition of positive interactions that act within populations, between species, and across scales from centimeters to hundreds of kilometers may greatly aid aquatic restoration efforts
- Positive interactions can often initiate crucially important recruitment and facilitation cascades, analogous to trophic cascades
- Ecological theory provides critical guidance for where and when positive interactions will be most important; management of physically and biologically harsh environments is likely to benefit the most from consideration of positive interactions

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Here, we propose a broader scope of positive interactions that acknowledges (1) how individuals within a population can benefit one another (intraspecific interactions) and (2) that positive interactions can be conducted across very large scales, even if individuals are never in contact (Table 1). Minimum population sizes that avoid Allee effects (positive relationship between population density and the reproduction and survival of individuals) and positive density dependence (eg spawning aggregations) are clear examples of the former, while cross-ecosystem linkages and subsidies that derive from species in one ecosystem and benefit other species in distant ecosystems illustrate the latter. These examples meet the traditional definition of positive interactions, in that one individual or species benefits without harm to the other, but expand the nature and scale of our traditional understanding of positive interactions.

We review how restoration and conservation have been conducted in the past, reflect on how terrestrial restoration efforts have benefited from consideration of positive interactions, and assess how aquatic management may also benefit from the explicit inclusion of positive interactions. We use our broader definition of positive interactions to explore how this inclusion can enhance the effectiveness and efficiency of restoration and conservation and, in particular, we evaluate where and when positive interactions need to take center stage in aquatic conservation and restoration efforts. Not all restoration and conservation efforts can benefit from inclusion of positive interactions, but all can profit from a more deliberate consideration of such relationships.

■ Past approaches to restoration and conservation

Conservation and restoration efforts focus on maintaining species, communities, or ecosystems to preserve ecosystem services (eg species diversity, water filtration) or function (eg nutrient cycling). Although the goals of conservation and restoration efforts may differ, the underlying ecological theory that determines their success or failure is similar. Traditional approaches generally focus on removing threats (eg pressure from predation, competition, or physical stress that affects mortality or reproduction), restocking or replanting threatened species, or setting aside protected areas based on organism home-range sizes and population distributions (reviewed in Young *et al.* 2005). These approaches are largely based on managing negative interactions. When positive interactions are addressed in terrestrial restoration projects, it is often through the use of nurse plants, foundation species, or non-native plantations to restore understory and faunal diversity (eg Parrotta *et al.* 1997; Padilla and Pugnaire 2006).

When positive interactions have been considered in aquatic conservation, focus has remained primarily on Allee effects for endangered species and on re-establishing foundation species (eg replanting salt marsh or sea grasses, building artificial reefs), which then provide habitat for other species to return, re-establish, and ultimately recover (eg Ehrenfeld and Toth 1997; Orth *et al.* 2002; Hassett *et al.* 2005). For example, coral reef restoration often focuses on building artificial reefs or on transplanting corals (Abelson 2006). However, such exploitation of positive interactions is rarely incorporated explicitly into management plans (Caughley 1994; Young *et al.* 2005); its application is generally ad hoc, and other types of positive interactions, such as the positive density dependence effects that mitigate abiotic and biotic stress to individuals (Bertness and Leonard 1997; Bruno *et al.* 2003), are also not generally addressed (Kaiser 2001). For salt marsh restoration, recent research suggests that success requires that: (1) marsh grasses are of sufficient height and density to be used by key marsh species; (2) soil grain size is appropriate for nitrogen retention to promote plant growth; (3) key marsh predators (eg blue crabs) are common enough

Table 1. Positive interactions and their implications for restoration and conservation

Category	*Example*	*Where and/or when important for restoration and conservation*	*Implications for the practice of restoration and conservation*
Traditional interactions	Facilitation	When species are dependent on biotic or abiotic conditions to recruit/survive	Protect foundation species and promote facilitation cascades; recognize that undesirable outcomes can also be facilitated
	Foundation species	Restoring species dependent on habitat provided by foundation species	Incorporate foundation and ecosystem engineer species into plans
	Mutualisms and commensalisms	Managing target species that require other species for recruitment, growth, or survival	Include and account for indirect interactions
	Succession	Ecosystem stability is management goal	Manage for dynamic systems
Within-population interactions	Allee effects	Protection of rare/endangered species or small, isolated populations	Protect and/or restore minimum population sizes
	Density-dependent recruitment and reproduction	When target species are recruitment limited	Protect aggregation sites or high abundance sites when appropriate
Large-scale interactions	Resource subsidies between ecosystems	Choosing locations for new restoration or mitigation sites	Account for spatial relationship of ecosystems and asymmetric pathways of resource exchange
	Ontogenetic habitat shifts	Target species use(s) multiple habitats during life history	Explicitly account for species and processes that connect ecosystems
	Protection of neighboring ecosystems	Managing ecosystems sensitive to external abiotic factors (such as storm disturbance)	Spatial management (such as reserves) should account for proximity and location of other ecosystems

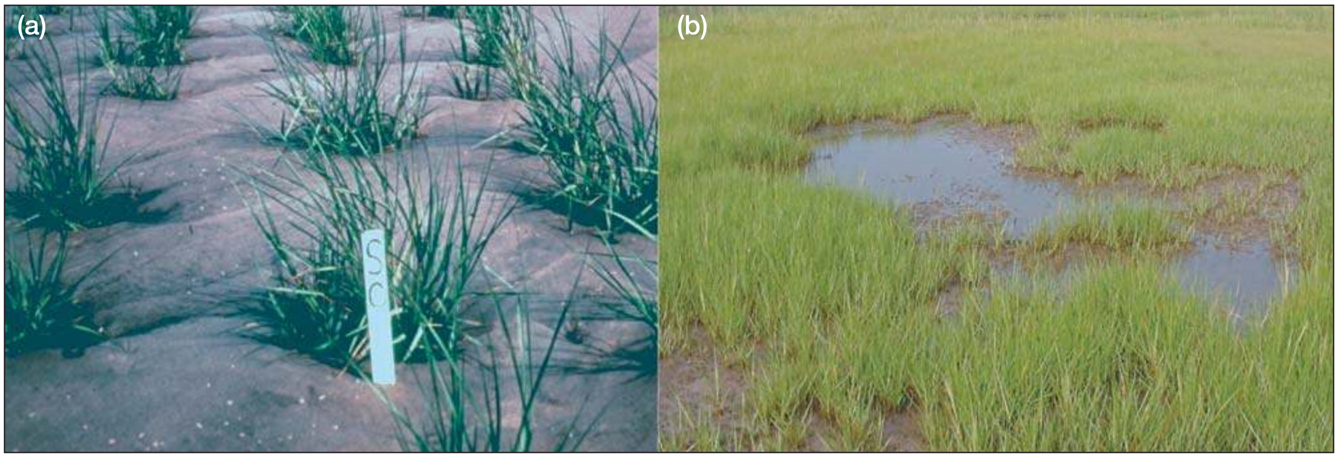

Figure 1. *Salt marsh restoration efforts that focus on (a) minimizing competitive interactions by creating small, evenly spaced clumps of grass versus (b) maximizing positive interactions by creating large patches in which plants ameliorate soil conditions for nearby plants, promoting growth.*

to suppress herbivorous snails that can kill marsh grass; (4) culms (stems of grass) are planted close together in the harsh anoxic mud, to facilitate shading and aeration of the soil; and (5) mycorrhizal fungi, which are crucial for plant growth, be artificially added, since they can take a long time to recruit naturally (Boyer and Zedler 1998; Pennings and Bertness 2000; Silliman and Bertness 2002). Despite these findings, most marsh restoration efforts simply involve the re-planting of small (< 5 cm in diameter) culms of grass on mudflats at evenly spaced intervals to avoid, theoretically, the negative impacts of inter-culm competition (Figure 1).

Similar approaches to restoration are seen in freshwater ecosystems, where macrophytes are established in nearshore areas of unvegetated reservoirs to provide nursery habitat or to encourage systems to switch from a turbid, filamentous algae-dominated state to a clear-water, macrophyte-dominated state (Moss 1990). These restoration activities include planting founder colonies of aquatic plants in small clumps (Smart *et al.* 1998) that are evenly spaced to reduce herbivory (predominantly from large herbivores like carp) and biotic disturbance. While this spacing of plants reduces competition for sediment-based nutrients (McCreary 1991), the choice of plant species and the potential role of positive interactions are largely overlooked. There are many types of aquatic macrophytes, including emergent, floating-leaved, free-floating, and submerged, and the specific species composition of the planted macrophytes may dictate the magnitude of positive versus negative interactions. Combinations of floating and submerged macrophytes may facilitate growth of both types (Agami and Waisel 1985), allowing founder colonies to spread more quickly to adjacent, unvegetated areas.

Because restoration tends to be carried out at the scale of small habitat patches (typically a few acres) mandated as mitigation for development that destroys habitat elsewhere (eg NRC 2001), the use of positive interactions in management plans is limited to processes that act at this scale. As human populations grow, as natural ecosystems continue to disappear, and as managers become more aware of interconnections among ecosystems, restoration efforts are becoming larger and more complex. In the US, large-scale efforts are underway to restore San Francisco Bay, the Chesapeake Bay, and the Florida Everglades. However, even these larger restoration efforts have focused on mitigating a few key threats and (re)introducing a few select species. In San Francisco Bay, a three-tiered approach to restoration includes limiting human access (threat mitigation), maintaining flood management (a service provided to society by the system), and habitat restoration, implemented primarily by adding landfill and planting marsh grasses (USFWS 2006). Positive interactions have not been explicitly considered. It is not only the presence of habitat-forming species and the area they need to grow that matters, but also the characteristics of those species and landscapes that will enable the most effective restoration (Bruno and Bertness 2001).

■ Positive interactions in restoration and conservation

Positive interactions act within and among populations and species and across a wide range of scales (Table 1), but may not be useful in all restoration and conservation efforts. We have developed guidelines for where and when management could benefit from incorporation of these different types of positive interactions at a variety of scales, and provide examples of how their inclusion can lead to fundamentally different approaches to habitat restoration, design criteria for protected areas, and strategies for abating or minimizing anthropogenic disturbances.

Traditional positive interspecific interactions

Most research on positive interactions and their structuring role for communities has focused on mutualisms, commensalisms, and foundation species (primary producers that are dominant in an ecosystem, both in terms of

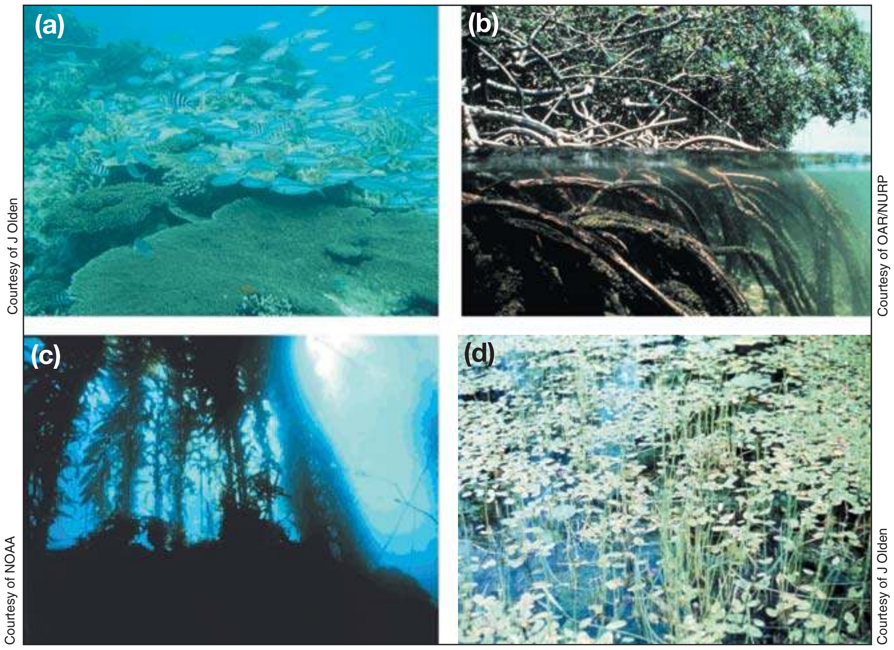

Figure 2. *Examples of foundation species that define ecosystems: (a) corals, (b) mangroves, (c) giant kelp, and (d) freshwater macroalgae.*

abundance and influence; Boucher *et al.* 1982; Ellison *et al.* 2005). Foundation species are particularly important for restoration because they can facilitate the colonization of other species by maintaining or providing key habitat or promoting community-level recovery from disturbance (eg Brady *et al.* 2002; Figure 2). Indeed, restoration often leverages this type of positive interaction. For example, facilitation is critical for coral reef maintenance, in that grazing species such as *Diadema* urchins and scarid fishes suppress the algae that would otherwise inhibit coral recruitment (Edmunds and Carpenter 2001). Restoring and protecting herbivores is therefore likely to be more important than protecting top trophic levels (eg predators) on coral reefs. Facilitation can also be indirect, as in trophic cascades, in which autotrophs benefit from predator effects on key herbivores, and may not always have ecosystem-scale positive effects. When plant abundance is a desired ecosystem state (as in kelp forest or seagrass systems), such facilitation would be viewed as positive for the ecosystem, but it would be negative where algal abundance is detrimental (as in coral reefs overgrown by algae).

Interestingly, management efforts have begun to move away from attempts to restore ecosystems to a pristine condition and toward restoring ecosystem function and services (Palmer *et al.* 2004). This new approach creates the opportunity to accelerate ecosystem recovery using non-native species but in turn raises the challenge of balancing this opportunity with maintenance of a primarily native community. The appropriate choice will depend in large part on management goals (D'Antonio and Meyerson 2002). One example of such a management decision is the proposed introduction of non-native oysters to the Chesapeake Bay to restore water quality and key habitat (Ewel and Putz 2004). Just as any competitor or predator of the management target species must be controlled to ensure that goals are met, any species that facilitates the recovery and survival of the management target species should be promoted. The potential for exotic species to benefit restoration through positive interactions has been recognized in terrestrial systems (Perrow and Davy 2002), but is less common in freshwater and marine systems. However, exotic species may drive species other than management targets locally or even globally extinct, even if indirectly (Gurevitch and Padilla 2004), and may create the potential for "invasional meltdowns" (sensu Simberloff and Von Holle 1999). This potential impact is still being debated, but has made exotic species a primary target for removal and a controversial restoration tool.

Including population-level interactions

Density dependence in population dynamics is typically seen as a negative force, as with density-dependent mortality. However, minimum densities are often necessary for population persistence (or growth), so that intraspecific interactions can be positive and exceed negative effects (eg Leslie 2005). Population-level positive interactions include minimum population sizes (ie avoiding Allee effects), conspecific cues that positively influence recruitment and survival of young (eg Courchamp *et al.* 1999; Greene and Stamps 2001), individual buffering of neighbors from harsh physical and biological stresses (eg Bertness and Leonard 1997), and conspecific aggregations for feeding, reproduction, or protection.

Conservation scientists have long recognized the importance of Allee effects, mainly because small populations of endangered and rare species are at risk of being eliminated as a result of fluctuating environmental conditions (Soule 1987; Henle *et al.* 2004). The protection of spawning aggregations or nesting sites is also a common conservation strategy (eg Beets and Friedlander 1999), but such efforts usually arise because managers believe that these events (ie reproduction) constitute population bottlenecks or present an opportunity to protect a wide-roaming or migratory species in a small, fixed area. This approach may be effective, yet restoration efforts focused on protecting aggregations would have very different strategies if their guiding principle were to maximize the positive density dependence that occurs at these aggregations versus, for example, minimizing the total area included in a protected area (Reed and Dobson 1993). For example, if breeding success increases with the total number of individuals at a site, a larger area with the same number of individuals as two smaller areas could constitute a much better conservation investment because of enhanced reproductive success.

Aquatic restoration efforts also rarely acknowledge that conspecifics may create a more attractive or hospitable environment for later arrivals. By promoting species that respond to conspecific cues, restoration efforts could establish a "recruitment cascade" that would enable more rapid establishment of stable populations. For example, oysters often recruit to the shells of conspecifics more readily than to other substrates (O'Beirn *et al.* 2000). If individuals also provide buffering from abiotic stress, then the success and stability of these populations might be even greater. Ecosystem-engineering species, which modify, maintain, or create habitat (for their own species and others) by changing biotic or abiotic conditions (Jones *et al.* 1997), can in some cases ameliorate harsh conditions. Not all species have population-level responses to such cues, but conspecific cues occur in a wide variety of taxa, including crabs (O'Connor and Van 2006), limpets (Zhao and Qian 2002), fishes (Griffiths 2003), and barnacles (Berntsson *et al.* 2004). Incorporating these dynamics into restoration and conservation plans could inform the choice of sites to protect (particularly for foundation and other engineering species) and species to target, as well as the overall goals.

Recognizing larger-scale interactions

There is a rich body of literature documenting how ecosystems are linked and can provide important subsidies to one another (reviewed in Polis *et al.* [1997]). Resources are often transferred between ecosystems via species migrations or transport of organic nutrients, providing supplements to local productivity. For example, oceanic salmon increase productivity of the river and forest ecosystems in which they spawn, die, and decompose (Helfield and Naiman 2001), while riparian vegetation returns productivity to streams and rivers through detrital input (Palmer *et al.* 2005). Similarly, species in mangroves and seagrass beds improve productivity of Caribbean coral reefs (Mumby *et al.* 2004), and salt marshes act as buffers, reducing the transfer of nutrients between land and sea (McClelland and Valiela 1998). Ecosystems are also connected through migrations between life-stages of a species; for example, river, estuarine, mangrove, and seagrass ecosystems all have nursery functions for many species that spend their adult lives in coral and rocky reef habitats (Beck *et al.* 2001). These interactions enhance productivity of nearby ecosystems by providing recruits to populations.

At a more local scale, restoration can be improved by harnessing positive interactions between species that stabilize community dynamics, ecosystem functions, and the structure of neighboring ecosystems (eg Cardinale *et al.* 2002). Species in riparian ecosystems help to stabilize stream and river shorelines, maintaining clear water and benthic habitats for other species dependent on such conditions (Naiman *et al.* 2005); coral reefs, mangroves, and salt marshes protect coastal habitats from storm damage (eg Sheppard *et al.* 2005). The 2004 Indonesian tsunami and Hurricane Katrina provided examples of how healthy shoreline ecosystems can protect inland areas (Bohannon and Enserink 2005; Danielsen *et al.* 2005)

The transfer of these concepts into restoration and conservation action is straightforward (Table 1). Most reserve network designs focus on connections between reserves, but not connections among species in different ecosystems within individual reserves or across the reserve network (Margules and Pressey 2000). The importance of land–sea connections and the role of positive interactions in enhancing conservation across these boundaries are just now becoming understood (Stoms *et al.* 2005), and require greater recognition in management efforts. Essentially, broadening the scale at which positive interactions are viewed requires attention to two core principles: (1) species that connect ecosystems deserve particular attention (eg salmon, nursery species, or migratory species) and (2) the spatial arrangement of different ecosystems is fundamental to reserve design and management plans.

■ Where and when are positive interactions important?

As with any ecological process, the importance of positive interactions for conservation and restoration will vary across space and time. Symbiotic relationships might be more important or common in some ecosystems (Bertness and Callaway 1994), and early successional species can have a greater impact on restoration efforts at the start of the process. Some species can compete with or facilitate each other, depending on the environmental context (facilitative inclusion versus competitive exclusion), so that fluctuations in environmental conditions can result in switches between positive and negative interactions. Determining if and where restoration and conservation can benefit from positive interactions should be a primary goal for future research. We provide some initial guidelines below.

Positive interactions should be particularly important for managing systems that are stressful to other species. Halophytic plant communities on cobble beaches and salt marshes, the distinct zone of sessile organisms on upper-intertidal shores, and hydrologically dynamic arid streams are all examples of physically stressful systems; coral reefs and other habitats under high consumer pressure are examples of biotically stressful systems. These ecosystems are largely dependent on the amelioration of stress by the physical habitat and provision of refugia from predation for successful functioning (Bertness and Callaway 1994; Bertness and Leonard 1997). In contrast, management plans are likely to benefit much less from positive interactions in physically or biologically mild

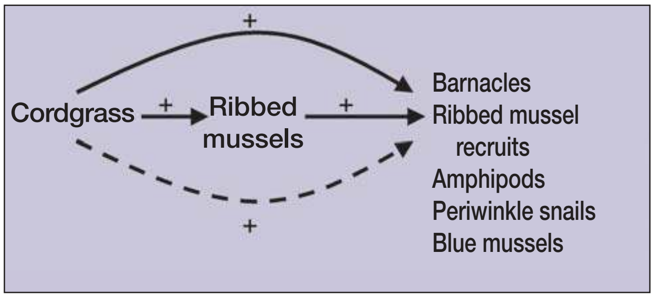

Figure 3. *A schematic of the facilitation cascade for the New England cordgrass system. In this system, the restoration of cordgrass facilitates the settlement and growth of ribbed mussels, which in turn provide hard substrate on which many other species can establish and survive. Cordgrass also provides direct facilitation to many of these species. Solid arrows represent direct effects and dashed arrows represent indirect effects.*

habitats, such as soft benthic marine and lake ecosystems. How stressful a system needs to be before positive interactions become important in driving system dynamics remains a pressing basic research question.

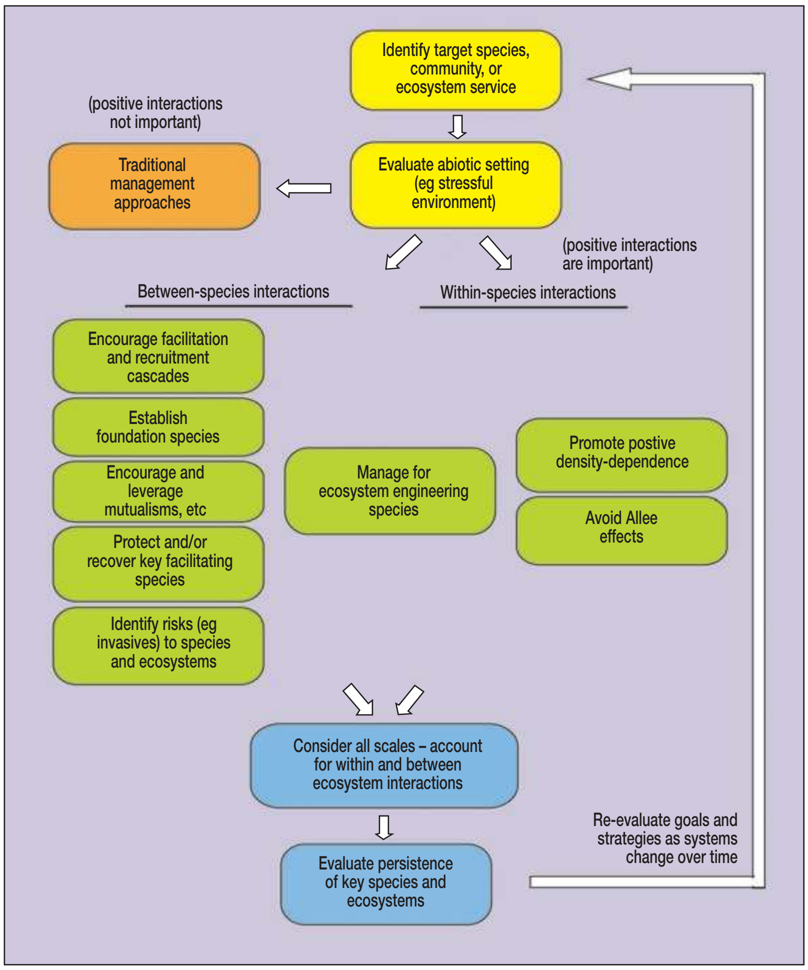

Figure 4. *A theoretical framework, or flow diagram, for incorporating positive interactions into restoration and conservation. Once target species and/or ecosystem services have been identified for conservation, managers should identify key positive interactions at all scales that, if promoted through policy and implementation, will facilitate preservation of the management target.*

Understanding the importance of temporal patterns within positive interactions can enable conservation biologists to harness processes such as "facilitation cascades" (eg facilitation between two species enables facilitation among other species) in future restoration efforts. In New England, for example, a facilitation cascade occurs when cordgrass stabilizes and shades substrate, allowing ribbed mussels to colonize the area, which in turn facilitates a rich invertebrate and algal community by providing a rock-like substrate for attachment (Altieri *et al.* 2007; Figure 3). Restoration and conservation in habitats based on foundation species should benefit greatly from incorporating facilitation cascades into management plans.

Given the complexity of ecosystems, it is not possible to prescribe exactly how best to incorporate positive interactions across all possible management plans. Management goals may require a focus on a particular species or ecosystem function, even if that focus is not ideal for the ecosystem as a whole. Furthermore, because the relative importance of positive interactions varies spatially and temporally, positive interactions may not be important for achieving management goals at certain locations and times. Perhaps most challenging, and an important area for future research, is that there are likely to be tradeoffs between different consequences of positive interactions, as with any set of interactions. For example, management could focus on restoring nearby ecosystems to allow for productivity subsidies among ecosystems, but this might facilitate the recruitment and growth of an invasive species targeted for removal. The relative importance of these different positive interactions is certain to be context dependent, but understanding this importance will be critical for determining the most effective and appropriate management strategies.

Despite these complexities, there are a number of ways in which positive interactions can easily be included in management plans (Figure 4). Foundation species should be initially identified, and the stressors they ameliorate and the species they facilitate listed. Managers can then choose targets and set goals based on the attributes of the foundation species in their system. Once these goals are set, managers can identify appropriate scales for meeting the goals (meters to thousands of kilometers, as in the salmon–riparian forest example), and then focus on the factors that facilitate the recruitment of key foundation species. Such factors might include indirect positive interactions conferred by species that remove competitors or consumers (eg trophic cascades) or that help ameliorate abiotic conditions for the foundation species (eg through ecosystem engineering), or the abiotic setting of the restoration site itself (eg oceanographic settings emerging from flow dynamics). In contrast, species conservation and restoration may benefit from a stronger focus on intraspecific interactions, such as positive density dependence and conspecific cues.

In any restoration project, there will be greater success if different initial approaches are tried experimentally, with the approach that produces the best response being adopted for larger-scale restoration. This strategy is particularly important for developing methods of incorporating positive interactions at particular locations, since the unique characteristics of a location will necessitate tailoring general rules to specific situations. In particular, adopting this strategy will require experiments that are designed to capture processes and their consequences at scales relevant to management (ie measurements in a few 1 m^2 plots will not be sufficient).

Conclusions

Although positive interactions might be part of many restoration and conservation plans, they are not currently being included or considered in proportion to their importance as ecological processes (Bruno *et al*. 2003). It is also unclear whether positive interactions, when included in management plans, are integrated on purpose; if not, it is unlikely that their use is optimal or that all types of interactions have been considered. It is one thing to say that positive interactions are captured by the plan, but quite another to design a plan to optimize the restoration or conservation benefits arising from positive interactions. Foundation species in particular merit much more attention in management plans, even if individuals of these species are abundant. Attention should continue to focus on minimum population sizes to avoid Allee effects and promote positive density dependence. Finally, the spatial arrangement of different ecosystems and the connections among those systems need to be explicitly recognized and incorporated into management plans, so that the benefits of restoration and conservation in one system can be leveraged to enhance nearby systems. Negative interactions have an important role in restoration and conservation efforts (humans are the ultimate predator and competitor for many systems), but positive interactions need a greater role if management is to achieve maximum success.

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