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Hierarchical Organization via a Facilitation Cascade in Intertidal Cordgrass Bed Communities

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abstract: It has recently been proposed that many communities are structured by a hierarchy of interactions in which facilitation by foundation species is of primary importance. We conducted the first explicit experimental test of this hypothesis by investigating the organization of positive interactions on New England cobblestone beaches. In this midintertidal community, wave-generated substrate instability and solar stress largely limit marine organisms to the shelter of cordgrass beds. Cordgrass, which can establish and persist without the aid of other foundation species, facilitates a dense assemblage of inhabitants (e.g., mussels, snails, seaweeds) with roots/rhizomes that stabilize substrate and a dense canopy that baffles waves and provides shade. Within the cordgrass bed community, ribbed mussels further enhance physical conditions and densities of other species (e.g., amphipods, barnacles) by providing crevice space and hard substrate. We conclude that cordgrass bed communities are hierarchically organized: secondary interactions (e.g., facilitation by ribbed mussels) play a key role within an assemblage dependent on primary facilitation by the independently successful foundation species cordgrass. Our results identify emergent indirect positive interactions in the form of facilitation cascades, have broad implications for conservation, and help unify existing models of community organization that were developed without considering the fundamental role of positive interactions.

Keywords: ecosystem engineers, facilitation cascade, foundation species, *Geukensia*, habitat restoration, hierarchical organization, *Spartina*, metacommunity, indirect interactions, positive interactions.

The fundamental role of positive interactions (e.g., mutualisms, habitat modification by foundation species sensu Dayton 1972) in structuring communities has recently been reemphasized and conceptually expanded (Callaway 1995; Power et al. 1996; Bertness and Leonard 1997; Hacker and Gaines 1997; Jones et al. 1997; Stachowicz 2001). However, most existing conceptual models of community organization do not incorporate positive interactions (Bruno et al. 2003). They have traditionally focused on physical factors such as resource levels and physical stresses and on other biological processes such as predation, competition, and recruitment. For example, Menge and Sutherland (1976, 1987) developed a general conceptual model that predicts how the importance of competition and predation in shaping communities varies as a function of environmental stress and recruitment. Tilman's (1982, 1990) resource competition models focused on resource competition among plants and later incorporated predation, disturbance, and recruitment (Holt et al. 1994; Tilman 1994). Hubbell's (2001) neutral model focuses on recruitment but does not consider the idiosyncratic and disproportionate effect of key community members such as foundation species in creating the communities to which the model is often applied. To make these established community models more reflective of the full set of factors that potentially structure natural systems, ecologists need to integrate and consider the relative role of positive interactions in both their conceptual and quantitative frameworks.

Bruno and colleagues (Bruno and Bertness 2001; Bruno et al. 2003) have begun this process by conceptually integrating positive interactions into many of the most commonly used models of community organization, including the niche theory, intermediate disturbance hypothesis, and Menge-Sutherland environmental stress model (Menge and Sutherland 1976, 1987). One of the more insightful hypotheses that was generated from this effort is that many communities are hierarchically organized by positive interactions. In such communities, facilitation by a foundation species (e.g., kelps, corals, tress) is the primary interaction that allows a suite of species to occupy a given

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habitat by ameliorating environmental stress, such as oxygenating the soil, buffering wave action, cooling the substrate, or limiting consumer pressure. Secondary factors like competition, predation, disturbance, and recruitment variation further shape community organization within the habitat provided by a foundation species.

The general dependence of species diversity and abundance on habitat created by living organisms has long been recognized (Holdridge 1947; MacArthur and MacArthur 1961; Whittaker 1975; Huston 1994). However, most theoretical models of community organization do not explicitly recognize the importance of foundation species and facilitation in general, because they are based on empirical studies that commonly focus on community interactions and ecosystem processes entirely within habitats created by foundation species (Bruno and Bertness 2001; Ellison et al. 2005). Hierarchical organization becomes apparent in many systems once the importance of habitat modification by a foundation species is considered, such as in river tussock systems where plant tussocks facilitate a community of epiphytic plants that are organized by chance and competition (Levine 2000). It is similarly apparent in submerged aquatic vegetation where small predators and their grazer prey are both dependent on the refuge from large predators provided by the vegetation (Heck and Crowder 1991). Hierarchical organization can also be observed in halophytic plant communities where vascular plants colonizing physically harsh habitats ameliorate the habitat for other plant species that compete for space in the created habitat (Bruno 2000; van de Koppel et al. 2006). Patches of such hierarchically organized communities that are interconnected via dispersal have been viewed as metacommunities (Wilson 1992; Leibold et al. 2004).

In addition to competition and predation, facilitation can be among the secondary interactions that structure communities within biogenic habitats. The general idea that communities are hierarchically organized can thus provide mechanistic insight into the specific case of communities associated with multiple foundation species. Many widely recognized biogenic habitats (e.g., coral reefs, mangrove forests, seagrass beds, conifer forests, grasslands) are structured by guilds of multiple foundation species that are often assumed to play either redundant or simply additive roles (Bruno and Bertness 2001). Jones et al. (1997), however, suggested that synergistic facilitation among habitat modifying species, which they broadly refer to as ecosystem engineers, is likely a widespread phenomenon of fundamental importance to community structure. They noted a lack of studies that employed the experimental approach necessary to rigorously investigate the separate and interactive effects of multiple foundation species, perhaps because a conceptual framework has been lacking to appropriately guide such investigations. An experimental test of hierarchical organization can help clarify whether multiple foundation species simply play an additive/redundant role or whether primary facilitation by a foundation species establishes a community in which other facilitators play important but secondary roles. Elucidating such interaction pathways and identifying key species in a community are essential to both build basic ecological knowledge and drive conservation efforts (Paine 1980; Mills et al. 1993; Menge 1995; Power et al. 1996).

In southern New England, where the harsh intertidal environment is typically composed of unconsolidated cobbles deposited by receding glaciers, cordgrass (*Spartina alterniflora*) and ribbed mussels (*Geukensia demissa*) are two dominant species (sensu Power et al. 1996) commonly found together in large, discreet beds that apparently work together to facilitate the intertidal community (fig. 1). To gain insight into this system with two foundation species and explore the nature of hierarchical organization in general, we tested the hypothesis that the cobble beach community within cordgrass beds is the product of one primary foundation species. Outside of beds, the beaches are composed of bare cobbles (5–25 cm in diameter) almost entirely free of organisms. Cobbles in these habitats can heat to >40°C on hot summer days (Bertness 1989), killing most sessile organisms, and cobble mobility during storms can crush and abrade any sessile and mobile organisms present (Sousa 1979; McGuinness 1987; Stephens and Bertness 1991). In contrast, the matrix of ribbed mussels coupled with a dense cordgrass canopy harbors a characteristic marine fauna and flora in which blue mussels (*Mytilus edulis*), acorn barnacles (*Semibalanus balanoides*), herbivorous periwinkle snails (*Littorina littorea*), gammarid amphipods (*Gammarus* spp.), and seaweeds (*Chondrus crispus* and *Ulva* spp.) are all abundant.

Both cordgrass and ribbed mussels have the potential to facilitate one another and associated organisms by buffering against solar stress and providing stable attachment substrate (Bertness 1984; Bertness and Grosholz 1985; Bertness and Leonard 1997; Bruno 2000). Only by experimentally manipulating the presence of one or both species and mimicking their physical attributes is it possible to determine whether a hierarchy of facilitative interactions gives rise to the cordgrass bed community. Do both ribbed mussels and cordgrass facilitate the community within beds, and if so, are their effects redundant? Does each foundation species facilitate the other on cobble beaches, or is there a hierarchy in which only one species is dependent on the other? We addressed these questions by conducting the first explicit experimental test of hierarchical organization by positive interactions in which secondary interactions occur within a community facilitated by a primary foundation species.

Figure 1: Photo of barnacle-encrusted ribbed mussels to edge of cordgrass bed in the midintertidal zone, with largely bare cobbles immediately adjacent. Photo was taken early in the growing season (May) as shoots of the perennial cordgrass were emerging. The shoreline runs parallel to the horizontal axis of the photo.

Methods

Study Area and Cobble Beach Community Surveys

All research was conducted on cobble beaches in Narragansett Bay, Rhode Island, a well-mixed estuary with near-oceanic salinity (28–31 ppt) and semidiurnal tides ranging from 0.8 to 2.0 m. To examine how community composition varied as a function of tidal height and cordgrass presence, we surveyed the percent cover of dominant organisms and bare substrate on cobbles in the low intertidal zone (mean lower low water) and inside and outside of cordgrass beds in the midintertidal zone of seven sites in July 2002: three sites each at Brown University Haffenreffer Reserve in Bristol (41°41′N, 71°14′W) and Narragansett Bay National Estuarine Research Reserve on Prudence Island (41°39′N, 71°21′W) and one site at Colt State Park in Bristol (41°41′N, 71°18′W). In each habitat, we estimated percent cover as the proportion of 100 points over a given category within each of 10 replicate 0.5-m^2 quadrats. All experiments were conducted on beaches within the Narragansett Bay National Estuarine Research Reserve.

Cobble Manipulation Experiment

We tested the hypothesis that sessile invertebrates are excluded from midintertidal cobbles by cobble instability and solar stress with a fully factorial experiment conducted from July 2002 to September 2004. Plots (60 cm × 60 cm, >1 m apart) were randomly assigned one level of cobble stabilization (stabilized or unmanipulated controls) and one level of shade (shaded or unmanipulated controls), with eight replicates of each combination (32 plots total). Cobbles were stabilized with vinyl-coated steel mesh (mesh size 2.5 cm) laid across the cobbles and held in place with rebar corner stakes (Bruno 2000). Plots were shaded with a double layer of black plastic mesh (mesh size 5 mm) held 30 cm above the plot by corner stakes (Bertness and Leonard 1997). A thermocouple (Omega model HH508) was used to quantify air, cobble (upper surface), and barnacle (body cavity) temperatures in each plot 3 h after emersion on a sunny day in July 2004. At the end of the experiment, we quantified invertebrate densities within a 25 × 25-cm quadrat centrally placed in each plot. Rapidly fleeing gammarid amphipods were noted as either present or absent within the quadrat, and barnacle densities were subsampled in an 8 × 8-cm area on a cobble surface. We defined ribbed and blue mussel individuals ≤15 mm as recruits.

Cordgrass Transplant Experiment

In May 2002–September 2004, we conducted a transplant experiment to examine whether nutrient limitation and/or habitat instability limited cordgrass establishment and persistence and to determine whether mussels could alleviate these potentially limiting stresses. Forty blocks of cordgrass and associated peat (30 cm^3) were cut from a fringing marsh and transplanted (>1 m apart) to the midintertidal of a cobble beach. Adult ribbed mussels were added to eight randomly selected replicates at densities typical of cordgrass beds (300–500 m^{-2}). Mussels were held in place with galvanized steel mesh (mesh size 2 cm) for 4 weeks until the mussels had attached to the substrate. In a fully factorial design, each of the remaining 32 blocks was randomly assigned one level of stabilization (stabilized or unmanipulated control) and one level of fertilization (fertilized or unmanipulated controls). Plots were stabilized as described above. Nutrients (Scott's slow-release Osmocote 14% by volume nitrogen, phosphate, and potassium) were delivered directly into the peat of fertilized plots through two 50-mL plastic screw cap centrifuge tubes (12–16 holes of 4-mm diameter drilled down the sides) in May 2002–2004. At the end of the experiment, we quantified the length of the longest rhizome and the density of stems, flowers, and aboveground biomass (after drying to a constant weight at 60°C) within a 25 × 25-cm quadrat centrally placed in each plot.

Cordgrass Bed Manipulation Experiment

From May 2003 to September 2004, we manipulated the cordgrass canopy and ribbed mussel densities in natural beds to examine their effects on one another and associated organisms. In a fully factorial design, 1-m^2 plots (>1 m apart) were randomly assigned one level of cordgrass canopy manipulation (aboveground biomass removed, aboveground biomass removed and replaced with a shade, or unmanipulated control) and one level of ribbed mussels manipulation (removed or unmanipulated control) for 12 replicates of each combination (72 plots total). Shades of black mesh, as described above, were suspended 60 cm above the plots by wooden stakes from April to October, when the cordgrass canopy is typically present. Cordgrass was removed by clipping and ribbed mussels were removed manually, and both were maintained as needed. We quantified treatment effects on the temperature of air, peat (1 cm below the surface), and body cavities of ribbed mussels and barnacles, as described above. At the end of the experiment, cordgrass performance and invertebrate densities were quantified as described above. Algae within the entire 1-m^2 plot was collected and weighed, and the number of Littorine snails on the algae was noted. To determine whether gradual loss of ribbed mussels in canopy removal and shade treatments could be explained by dislodgement, we quantified attachment strength of three mussels (5–6 cm) per plot in August 2004 (see methods in Carrington 2002).

Statistical Analysis

Data were analyzed with JMP 5.0 statistical software (SAS Institute, Cary, NC). All data were transformed as necessary to meet the assumptions of ANOVA. Post hoc analyses were by Tukey's HSD test. For survey data, quadrats were nested within their respective zones for each replicate site. For mussel attachment strength data, replicate plots were nested within cordgrass canopy treatment. Presence/absence data for gammarid amphipods were examined with χ^2 analyses. See tables A1–A6 in the online edition of the *American Naturalist* for ANOVA output tables.

Results

Cobble Beach Surveys

There was a striking difference between communities inside cordgrass beds and on cobbles at the same intertidal height (figs. 1, 2; table A1). At the midintertidal level, ribbed mussels, blue mussels, and algae were found exclusively within cordgrass beds, and barnacle cover was an order of magnitude higher in beds than on adjacent bare cobbles. Percent covers of both barnacles and algae were similar ($P > .05$ Tukey's HSD post hoc) to that of lower cobble, where blue mussels were also commonly found, indicating that the environment within beds is more similar to cobbles at less stressful lower tidal heights than to cobbles at the same height. In contrast to the habitat within cordgrass beds, midintertidal cobbles outside of cordgrass beds were almost entirely devoid of organisms.

Cobble Manipulation Experiment

Shading and stabilizing cobble in the midintertidal, where cordgrass beds occur, revealed that sessile invertebrate densities are limited by both solar stress and substrate stability. The shading treatment reduced solar stress by lowering both cobble ($F = 213.3$, df = 1, 28, $P < .0001$) and barnacle ($F = 466.6$, df = 1, 28, $P < .0001$) temperatures by ~8°C (fig. 3*a*; table A2). The only sessile invertebrates on cobbles were barnacles, and their densities were significantly higher when cobbles were shaded ($F = 170.8$, df = 1, 28, $P < .0001$) or stabilized ($F = 11.0$, df = 1, 28, $P < .05$; fig. 4*a*). Shading had the largest effect, with barnacle densities four

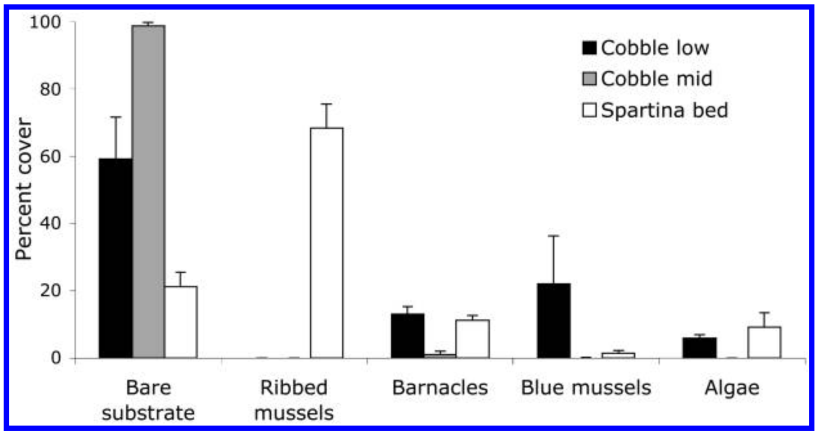

Figure 2: Percent cover dominant space holders in cordgrass beds, on cobble at the same midintertidal height as beds, and on cobble at lower tidal height. Data are shown as means + 1 SE of seven replicate sites.

to five times higher than stabilization alone (no significant treatment interaction). Adult ribbed mussels and blue mussel recruits were found among cobbles, and their densities were highest when cobbles were shaded ($F = 5.5$, df = 1, 28, $P < .05$ for both species) and unaffected by stabilization (fig. 4*a*; table A3). Densities of ribbed mussel recruits, blue mussels adults, and *Littorina* and the presence of amphipods did not differ among treatments ($F < 2.8$, df = 1, 28, $P > .10$ for all analyses).

Cordgrass Transplant Experiment

All but one of the 40 cordgrass transplants established and flourished over the three growing seasons. The one that failed had washed away in a storm within a month of transplanting and was excluded from further analyses. Mussels had no effect on any measures of cordgrass success, which included lateral extension, aboveground biomass, total stems density, and density of flowering stems ($F < 1.5$, df = 1, 13, $P > .25$ all analyses). Addition of fertilizer led to twofold to fourfold increases in aboveground biomass ($F = 44.2$, df = 1, 28, $P < .0001$), the density of flowering stems ($F = 14.7$, df = 1, 28, $P < .001$), and total stem density ($F = 109.9$, df = 1, 28, $P < .0001$; fig. 4*b*). Stabilization and treatment interactions had no effect on any of those responses ($F < 1.1$, df = 1, 28, $P > .32$ all analyses; table A4). The lateral extension of cordgrass transplants (vegetative growth) was not influenced by experimental treatment ($F < 2.0$, df = 1, 28, $P > 2.0$ all analyses).

Cordgrass Bed Manipulation Experiment

Similar to the cordgrass transplant experiment, the presence of ribbed mussels did not affect aboveground biomass, total stem density, or flowering stem density of cordgrass in naturally occurring beds ($F < 1.3$, df = 1, 22, $P > .27$ for all analyses).

The cordgrass canopy reduced temperatures of peat ($F = 111.1$, df = 2, 35, $P < .0001$), ribbed mussels ($F = 60.5$, df = 2, 35, $P < .0001$), and barnacles ($F = 38.0$, df = 2, 35, $P < .0001$) by ~6°–8°C, and the shade treatment mimicked that effect accurately (no Tukey's HSD post hoc difference between canopy and shade treatment; fig. 3*b*; table A5). Cordgrass had a significant ($F = 11.6$, df = 2, 33, $P < .001$) effect on the success of adult ribbed mussels that appeared primarily because of their dependence on canopy structure for attachment rather than shade. In treatments in which neither ribbed mussels nor the cordgrass canopy was experimentally manipulated, the average density of ribbed mussels was nearly twice that of the two experimental treatments in which the cordgrass canopy was removed, regardless of whether the canopy was experimentally replaced with a shade (no Tukey's HSD post hoc difference between canopy and shade treatment; fig. 5). Attrition of ribbed mussels in both cordgrass canopy removal treatments (with and without shade) can be explained by dislodgment, since the attachment strengths of ribbed mussels in the two treatments were similar (no Tukey's HSD post hoc difference), and both were significantly lower than the treatment in which the natural cordgrass canopy was present ($F = 9.7$, df = 2, 33, $P < .001$). This is a conservative result, since the most poorly attached individuals would already have been lost during the experiment.

The densities of ribbed mussel recruits and adult blue mussels were highest when ribbed mussels and cordgrass were not removed because of an interactive effect of those two factors ($F = 6.4$, df = 2, 66, $P < .01$; $F = 7.8$, df = 2, 66, $P < .001$, respectively), whereas blue mussel recruits

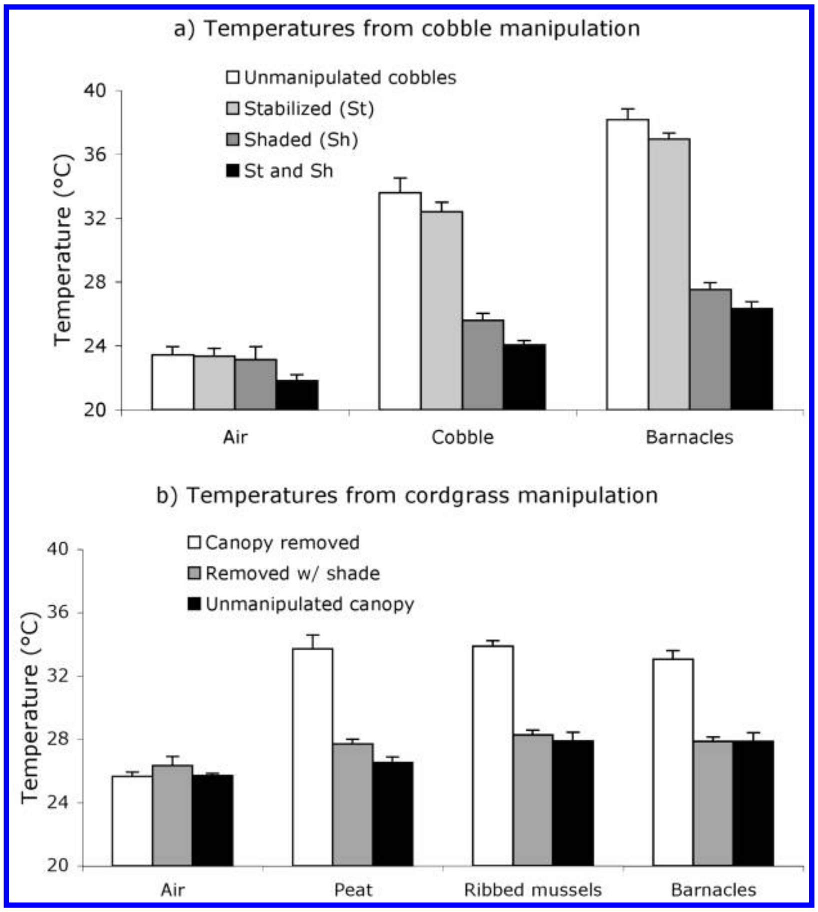

Figure 3: Temperatures of air, substrate, and epifauna from cobble manipulation (*a*) and cordgrass canopy manipulation (*b*) experiments. Data are shown as means + 1 SE of eight replicate plots.

and barnacles were most abundant because of an additive effect ($F > 9.1$, df = 2, 66, $P < .001$ all analyses; fig. 5; table A6). *Littorina* were more abundant when ribbed mussels were not removed ($F = 10.1$, df = 2, 66, $P < .01$), and their densities were not affected by cordgrass canopy treatment ($F = 1.6$, df = 2, 66, $P = .21$). Algal biomass was highest when the cordgrass canopy was not removed ($F = 72.0$, df = 2, 66, $P < .0001$; fig. 5). Algal biomass was detectably lower ($F = 4.8$, df = 2, 66, $P < .05$) when ribbed mussels were not removed (the only negative effect detected by our experimental manipulations), though that effect was clearly swamped by the positive effect of the cordgrass canopy (fig. 5). Gammarid amphipods were most commonly observed in plots in which ribbed mussels were unmanipulated and/or either the natural cordgrass canopy or shade mimic was present ($\chi^2 = 46.2$, df = 1, 70, $P < .0001$; fig. 5).

There was a strong positive correlation ($R^2 = 0.79$, $P < .0001$) between the biomass of algae in a plot and the number of *Littorina* inhabiting that algae. There was no effect of cordgrass canopy or ribbed mussel treatment on the density of *Littorina* standardized for algal biomass ($F < 2.9$, $P > .1$ all analyses).

Discussion

This study provides the first explicit experimental evidence of hierarchical organization in which secondary interactions occur embedded within a community that is principally dependent on facilitation by a foundation species. We found cordgrass to be a powerful foundation species that successfully established, persisted, and flourished on cobble beaches independently of other foundation species (e.g., ribbed mussels) found in the system. By stabilizing and shading the cobble substrate, cordgrass created an environment inhabited by a diverse and thriving community (including barnacles, ribbed mussels, blue mussels, two algal species, amphipods, and herbivorous snails) that

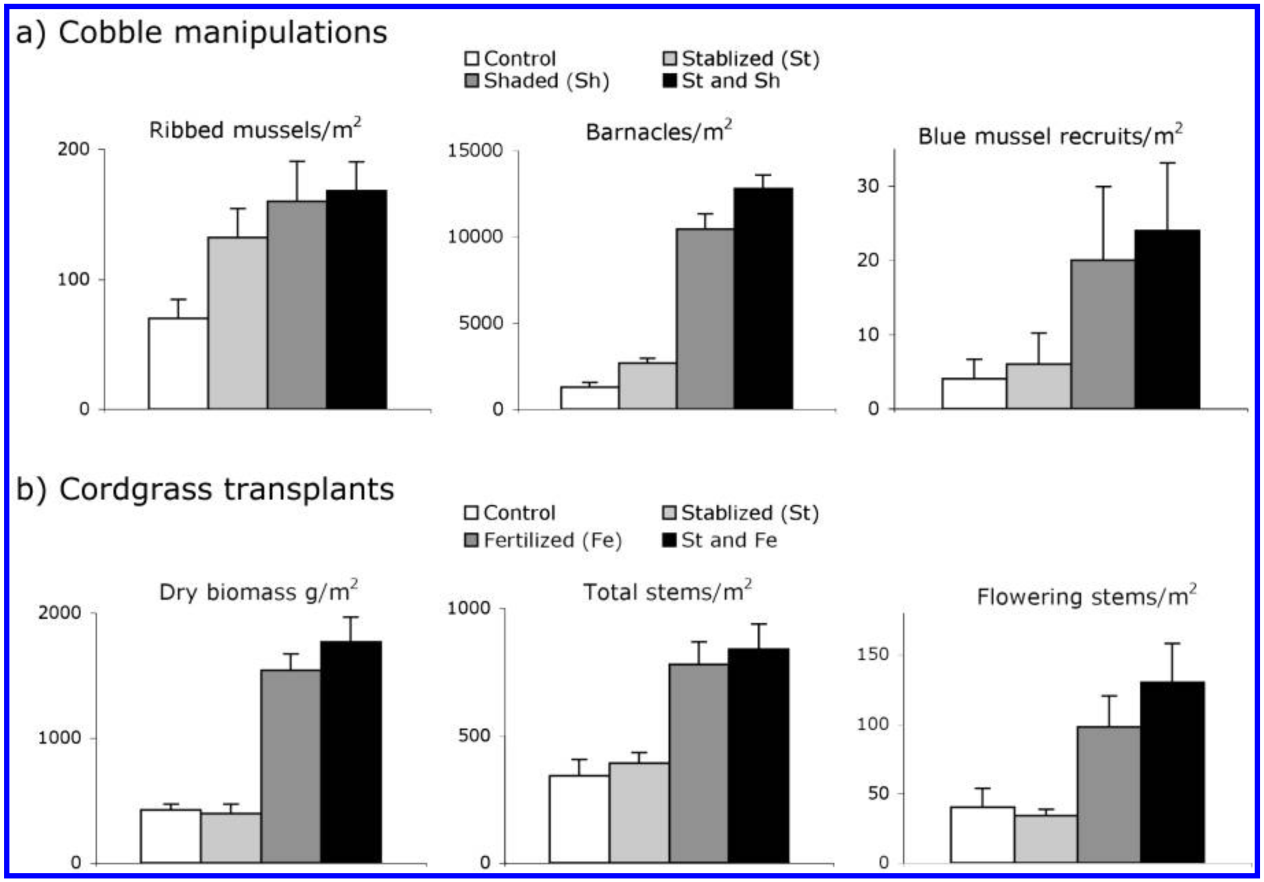

Figure 4: *a*, Abundance of invertebrates in cobble manipulation experiment. *b*, Establishment, growth, and reproductive effort of cordgrass in transplants experiment after three growing seasons. Data are shown as means + 1 SE of eight replicate plots.

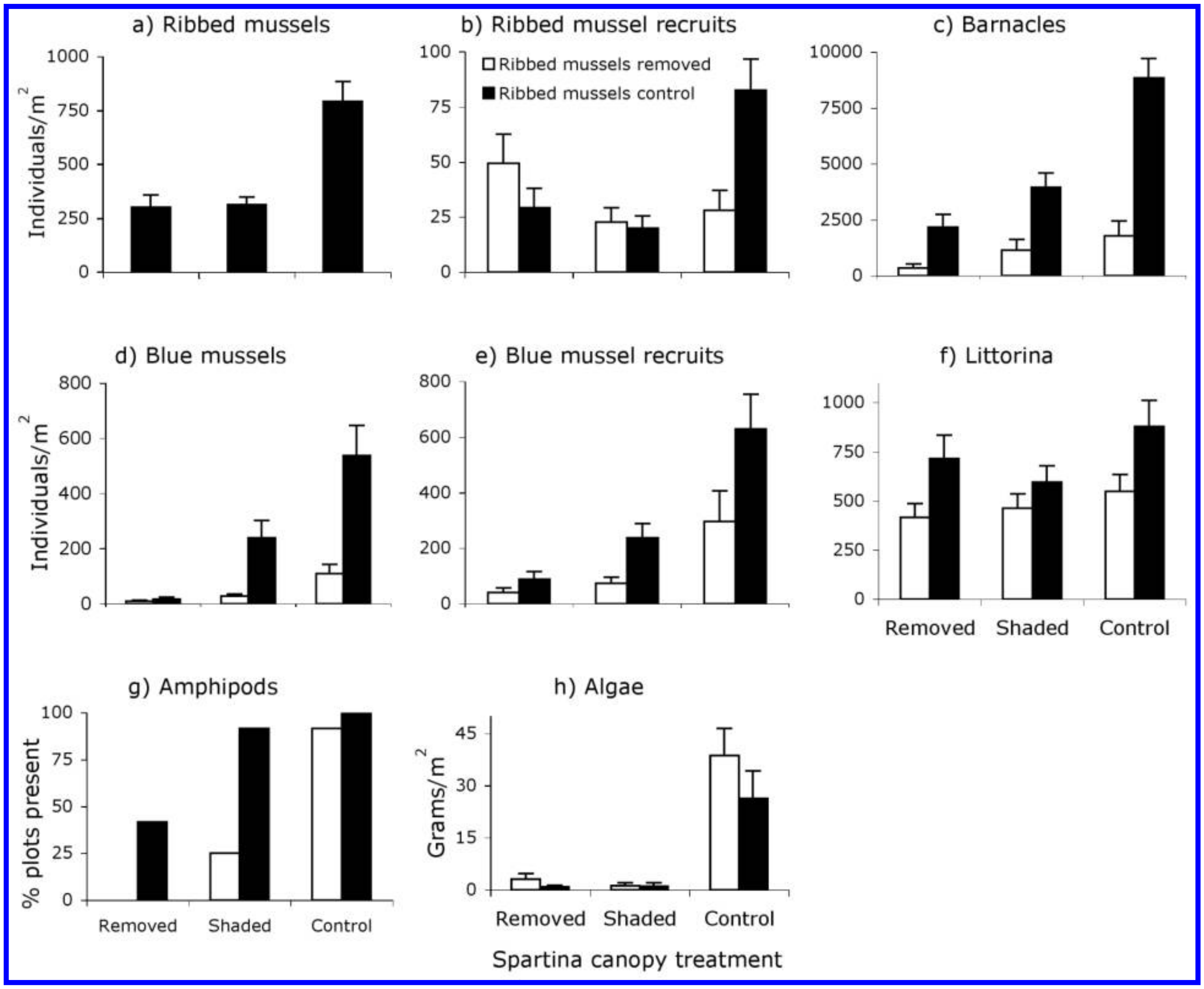

Figure 5: Response of invertebrate densities to manipulation of cordgrass canopy and ribbed mussels (*a–f*), percent of plots in which amphipods were found (*g*), and algal biomass response to manipulations (*h*). Data are shown as means + 1 SE of 12 replicate plots.

was largely absent from midintertidal cobbles outside of cordgrass beds because of environmental stress. Within this community dependent on cordgrass, ribbed mussels were a secondary foundation species that further enhanced physical conditions by providing crevice space and stable substrate and thereby had a positive effect on the abundance of bed inhabitants.

Mechanisms of Facilitation

Substrate instability and solar stress limited the distribution and abundance of intertidal organisms on cobble beaches (figs. 1, 2, 3*a*; Stephens and Bertness 1991; Bruno 2000). The cordgrass canopy can ameliorate those conditions by baffling wave disturbance of the substrate (Bruno 2000), providing stable attachment structure for mussels (fig. 5), shading the substrate (fig. 2; van de Koppel et al. 2006), and enhancing recruitment through the passive deposition of propagules (Eckman 1983; Bertness and Grosholz 1985; Bruno 2000). As a consequence, invertebrate and algal cover surveyed within cordgrass beds were much higher than on bare cobbles at the same tidal height, and the same or higher than that observed in the low intertidal (fig. 2). This suggests that cordgrass beds alleviated physical stress and extended the distribution of intertidal organisms in a manner similar to other foundation species, including ascidians (Castilla et al. 2004), *Mytilus* mussels (Suchanek 1986), and algal canopies (Dayton 1975; Bertness et al. 1999).

Within the community established by cordgrass, aggregations of ribbed mussels further improved physical conditions by buffering against temperature extremes (Bertness and Leonard 1997), providing hard attachment substrate utilized by barnacles, and creating crevice space inhabited by amphipods and blue mussels. Moreover, ribbed mussels may have increased the diversity and abundance of associated organisms by providing a refuge from predation, as observed in subtidal mussels beds (Witman 1985; Lindsey et al. 2006).

Our results indicate that cordgrass had only neutral or positive effects on members of the macrofauna and algae community of cobble beaches and did not appear to displace other species. However, in some instances, the primary foundation species that defines a community type may displace other species even while having an overall positive effect on biodiversity. For example, mussel beds on the rocky shores of the eastern Pacific competitively excluded algae, barnacles, and other invertebrates but provided habitat for a different assemblage of crevice-dwelling species with higher diversity (Paine 1966; Suchanek 1986).

Hierarchical Nature of Interactions

In a hierarchically organized community established by a foundation species (cordgrass in this case), the abundance of some or all inhabitants is dependent on interactions with one or more other inhabitants (ribbed mussels) that are themselves dependent on the primary foundation species (Bruno and Bertness 2001). Experimental manipulation of the hypothesized secondary interactor is necessary to identify the hierarchical nature of community organization since many species may appear dependent on the primary facilitator, even if indirectly via secondary interactions. The cordgrass bed manipulation experiment revealed a number of facilitative interactions within the vegetated community through the mechanisms of stress amelioration outlined above: (1) cordgrass had a positive effect on ribbed mussels and algae; (2) ribbed mussels had a positive effect on Littorine snails; (3) cordgrass and ribbed mussels each had a positive effect on the abundance of barnacles, blue mussel recruits, and amphipods; and (4) cordgrass and ribbed mussels had an interactive positive effect on the abundance of adult blue mussels and ribbed mussel recruits (fig. 5; table A6).

Though it was clear that both cordgrass and ribbed mussels had positive effects, it was the one-way facilitative relationship between these two foundation species that made the hierarchical organization of positive interactions within cordgrass bed communities apparent. We found that cordgrass independently established, grew, and reproduced on cobble beaches (fig. 4*b*). Mussels did not contribute to the success of cordgrass, despite our experimental evidence that cordgrass was nutrient limited on cobble beaches (fig. 4*b*) and that ribbed mussels enhanced cordgrass productivity in nearby low-flow marshes by providing nutrients (Bertness 1984). In contrast to the independent success of cordgrass, experiments in established cordgrass beds revealed that ribbed mussels were dependent on cordgrass (fig. 5). Both the abundance and attachment strength of ribbed mussels were significantly lower when the cordgrass canopy was removed with or without experimental shading, suggesting that attachment substrate, rather than the amelioration of solar stress, was the primary mechanism by which cordgrass facilitated ribbed mussels. In our surveys of cobble beaches, epifaunal ribbed mussels were observed only within cordgrass beds (figs. 1, 2), further underscoring the obligate dependence of ribbed mussels on cordgrass beds to form emergent structures capable of facilitating other species. Therefore, ribbed mussels, and their associated positive interactions, should be viewed in the context of occurring within the community facilitated by cordgrass.

We focused on secondary interactions that were facilitative in our test of hierarchical organization because we were interested in teasing apart the relative importance of two hypothesized foundation species in the cobble beach system. Indeed, facilitation was overwhelmingly important, with 12 out of 16 interactions experimentally examined within cordgrass beds found to be positive and only one negative. However, hierarchical organization can readily incorporate other secondary interactions within the community facilitated by cordgrass, such as crab predation on mussels, grazing by snails, and competition between barnacles and *Mytilus* mussels.

Hierarchically organized communities, which are primarily dependent on facilitation, are predicted to be most prominent either in relatively physically harsh environments, where foundation species play a crucial role of stress amelioration (as in this study), or in physically benign areas, where foundation species facilitate the community by providing a predation refuge (Bertness and Callaway 1994). In areas of intermediate environmental stress, factors other than facilitation, such as competition, are likely to play a dominant role in community structure (Menge and Sutherland 1976, 1987; Connell 1978; Bruno and Bertness 2001; Bruno et al. 2003).

Hierarchical organization by positive interactions allows for interpreting the relative importance of multiple community interactions that can co-occur during successional community development, in which early colonizers often facilitate other interacting species by ameliorating the harsh environment of a disturbed area or newly created habitat (Walker and Chapin 1987). However, succession, as classically defined, refers to specific cases with species replacing other species over time (Morin 1999), whereas hierarchical organization by positive interactions is a more general phenomenon that also includes instances (such as on cobble beaches) where the primary foundation species remains and is required for the community to persist.

Facilitation Cascade

The pattern of dependent positive interactions we observed in the cordgrass bed community is a subcategory of hierarchical organization that emerges within communities containing multiple facilitators. This suite of positive interactions is a facilitation cascade, in which the positive effects of a secondary facilitator are contingent on habitat amelioration by a primary foundation species. Stachowicz (2001) suggested broadly that the positive effects of one species on another could cascade through a community via other interactions. In a facilitation cascade, those secondary effects include the triggering of secondary positive interactions.

The chain of positive interactions and indirect effects in a facilitation cascade are analogous to the emergent interactions that arise from multiple consumers in a trophic cascade (Hairston et al. 1960) or multiple competitors in an intransitive competitive network (Buss and Jackson 1979). Trophic cascades have proven to be a general predictor of structure and productivity in systems as varied as kelp forests (Estes et al. 1998), salt marshes (Silliman and Bertness 2002), and lakes (Carpenter and Kitchell 1988). Likewise, intransitive networks are a common mechanism of coexistence and diversity, such as in microbial communities (Karolyi et al. 2005), insect guilds (Palmer 2004), and lizard mating systems (Sinervo and Lively 1996). We expect the facilitation cascade concept to have similarly broad explanatory power when incorporated into both empirical and theoretical studies.

Our results build on the conclusions of Power et al. (1996), who suggested that the productivity/standing crop necessary to form the significant structure of habitat-forming species is more likely to be found at basal trophic levels. Within hierarchically organized cordgrass beds, we found that the primary foundation species was a primary producer (cordgrass), the secondary facilitator was a primary consumer (ribbed mussels), and the inhabitant species benefiting from positive interactions were either primary or secondary consumers. The generality of this apparent correlation between trophic level and position within a facilitation cascade, first identified here in cordgrass beds, remains to be tested in other systems. If the pattern holds, it would have consequences for predicting the relationship between ecosystem productivity and the number/organization of foundation species in a system. Such a relationship could be explained in part by the attenuation of productivity with each succeeding trophic level (Lindeman 1942) and the resulting lower limits on biomass at each level limiting the role of a given foundation species.

Conservation Implications

Habitat modifying species are important targets for conservation because of their fundamental importance for community diversity and stability (Halpern et al., forthcoming; Mills et al. 1993) and their integral role in mediating environmental degradation (Altieri and Witman 2006). In hierarchically organized communities, particularly those with multiple facilitators, the limited resources of restoration and preservation efforts should be directed toward the primary foundation species, which gives rise to the assemblage of inhabitant species and secondary interactions. Similarly, efforts to eradicate exotic species should focus on primary foundation species since they are likely to have disproportionately large effects in invaded areas because of the secondary interactions of associated organisms, as apparently occurs with cordgrass outside its native range (Ayres et al. 2004; Neira et al. 2005; Levin et al. 2006). Hierarchical organization by positive interactions can explain the disruption of secondary biological interactions due to fragmentation of aquatic and terrestrial habitats (often defined by dominant vegetative foundation species) because the intensity of habitat modification by foundation species is often dependent on patch size (Forman and Godron 1981; Saunders et al. 1991; Hovel and Lipcius 2001), as observed for cordgrass in particular (Bruno and Kennedy 2000).

Conclusions

The general importance of hierarchical organization by positive interactions needs to be incorporated into our understanding of community assembly rules. Many empirical studies of competition and predation have focused on communities within habitats formed by foundation species such as kelp forests (Anderson 2001), coral reefs (Carr et al. 2002), oyster beds (Lenihan et al. 2001), riparian grasses (Levine 2000), and terrestrial plant communities (Holzapfel and Mahall 1999). As a consequence, most conceptual models have been derived from the within-habitat perspective and do not consider the context of the community itself (Leibold et al. 2004). Hierarchical organization by positive interactions reveals that the predictive power of conceptual models is often contingent on community establishment by facilitation and thus provides the biological basis for updating many conceptual models of community organization by integrating positive interactions with other ecological interactions (Bruno et al. 2003). This broad perspective reveals emergent mechanisms, including facilitation cascades, that are critical determinants of species diversity and abundance in a community and can play an important role in directing conservation efforts. Our study demonstrated that a manipulative experimental approach was necessary to elucidate the hierarchical nature of interactions that superficially appear to be codominant in communities. Additional experimental studies will help place many established mechanisms of community organization in the appropriate context of facilitation and will provide the basis for incorporating positive interactions into many of the models where they have been previously overlooked.

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