Trait-dependent modification of facilitation on cobble beaches

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Abstract. Fundamental gaps remain in our knowledge of how positive species interactions, such as facilitation and mutualism, structure and maintain populations and communities. Foundation species create extensive biogenic habitats, but we know little of how their traits, such as density, age, and patch size, modify their ability to facilitate other species. We tested the role of facilitator traits in cobble beach plant communities in New England, USA. In this system, intertidal beds of the cordgrass *Spartina alterniflora* facilitate populations of halophytic forbs at higher shore elevations by buffering wave action, stabilizing cobbles, and limiting physical disturbance. Using descriptive and experimental techniques, we tested the hypotheses that (1) the density and height of cordgrass shoots modify the strength of the cordgrass–forb facilitation, and (2) cordgrass peat alone contributes to the facilitation of forbs. Increased shoot density, as well as the combination of cordgrass peat and shoots, positively affected two life history stages (seedling and adult) of the abundant forb *Suaeda linearis*, demonstrating that cordgrass traits modify the strength of facilitation in this system. Since the expression of traits varies within and among patches of any given foundation species, traits can and should be used to predict the strength of facilitation, to guide the development of conservation strategies, and to develop more accurate models of species interactions.

Key words: cobble beach; facilitation; foundation species; habitat; *Spartina alterniflora*; species interaction; *Suaeda linearis*.

INTRODUCTION

Species interactions are central for shaping patterns of distribution and abundance, and to theories of community dynamics (e.g., Paine 1980, Menge and Sutherland 1987, Tilman 1994). Interactions range from negative to positive, but ecologists have historically focused on negative interactions, such as competition and predation, as key structuring forces (Hairston et al. 1960, Tilman 1982, Keddy 2001). Positive species interactions, such as facilitation and mutualism, have long been recognized (Clements 1916), but their role in shaping communities has only recently been appreciated (see reviews by Bertness and Callaway 1994, Callaway 1995, Stachowicz 2001, Bruno et al. 2003). Notable theoretical cornerstones, including niche theory, the intermediate disturbance hypothesis, and environmental stress gradients, require substantial rethinking when positive interactions are considered (Bruno et al. 2003).

Facilitation through biogenic habitat provision is a widespread type of positive interaction. By growing and completing their life cycle, foundation species (sensu Dayton 1972) such as trees, shrubs, salt marsh grasses, corals, kelps, seagrasses, and mussels, create extensive habitats that enhance the fitness and distribution of other species directly, by providing living space and food resources, and indirectly, by providing refuge from predators and abiotic stress (Jones et al. 1994, Bruno and Bertness 2001, Grutter and Irving 2007). The subsequent ensembles of negative and positive interactions among facilitated species (Altieri et al. 2007) cumulatively affect emergent ecosystem properties such as productivity, nutrient cycling, and diversity (Stachowicz 2001).

While facilitation by most foundation species is recognized, we know little of how their individual- and population-level traits modify the strength of facilitation (i.e., the amount by which environmental conditions are modified and other taxa are facilitated; Bruno and Bertness 2001). Trait variation can change the amount of habitable space, resource availability, and amelioration of environmental stress (Gleason et al. 1979, Leonard and Luther 1995), and may therefore substantially modify the strength of facilitation. For example, population-level traits such as plant density, aboveground biomass, and patch orientation to prevailing currents can all modify the ability of seagrass beds to facilitate fish and invertebrates (Heck and Wetstone 1977, Fonseca et al. 1996, Tanner 2003), while long-term declines in fish abundance and diversity occur when coral biomass and complexity are reduced (Sym and Jones 2000). In terrestrial environments, the individual-level trait of a plant’s canopy architecture can influence the degree of environmental modification (e.g., shading) and therefore modify its potential as a nurse plant.
Overall, however, rigorous experimental evidence of the role of facilitator traits is lacking for most systems (Bruno and Bertness 2001). Such knowledge would nevertheless be useful for developing facilitation theory, predicting community structure under altered environmental conditions, and for identifying conservation priorities.

The purpose of this study was to address this knowledge gap in a system where underlying facilitative mechanisms are understood. On cobble beaches in New England, USA, the cordgrass Spartina alterniflora forms extensive intertidal beds of dense peat and seasonal aboveground shoots (April–October) that create habitat for marine mussels, barnacles, gastropods, amphipods, crabs, and algae (Altieri et al. 2007). Beds longer than ~25 m also facilitate communities of annual and perennial halophytic forbs higher on the shore by buffering wave energy, stabilizing cobbles, and limiting burial and disturbance at critical early life history stages of forb seedling emergence and establishment (Bruno 2000, Bruno and Kennedy 2000; see Plate 1 and Appendix A). In the absence of cordgrass, or when beds are shorter than 25 m, forbs germinate but even the most tolerant species are unable to establish because of physical disturbance from unstable cobbles (Bruno 2000, Bruno and Kennedy 2000).

The dependence of forbs on cordgrass beds greater than 25 m in length already demonstrates a trait-dependent threshold for facilitation (i.e., patch size: Bruno and Kennedy 2000), yet within and among these larger beds, other population-level traits such as cordgrass shoot density and height can vary greatly. Variation of these traits alters hydrodynamics and sediment accretion within cordgrass beds (Gleason et al. 1979, Leonard and Luther 1995), making it possible that the facilitation of forbs is also affected, given their reliance on the reduction of wave energy by cordgrass (Bruno 2000). To explore this question, we correlativey examined the relationship of forb abundance with cordgrass shoot density and height, and then experimentally manipulated shoot density and height to test the hypothesis that these two population-level traits modify cordgrass facilitation of forbs (survival and per capita biomass).

In addition to cordgrass shoots, the peat base may contribute to forb facilitation because it can form a distinct wall up to ~1 m tall that buffers wave energy and stabilizes cobbles (A. Irving and M. Bertness, personal observations). The peat base mostly comprises compacted layers of dead cordgrass shoots and roots that slowly accrete over time, and within which the short shallow roots of living cordgrass can anchor. Living cordgrass root biomass forms a relatively minor component of peat, so while the peat is an integral part of the entire cordgrass bed, it could be considered a distinct structural element in the context of the cordgrass–forb facilitation. Indeed, an earlier experiment that removed cordgrass shoots (i.e., leaving only peat) found that water flow and cobble instability increased relative to areas where cordgrass remained intact, but were still below levels observed in the absence of cordgrass beds (termed “interbed” habitats; Bruno and Kennedy 2000). Even so, the relative contribution of peat to the cordgrass–forb facilitation is unknown, so the hypothesis that cordgrass peat contributes to the facilitation of cobble beach forbs was tested by experimentally removing shoots (leaving peat) and comparing forb survival and per capita biomass to those behind intact shoots and to those in interbed habitats.

Materials and Methods

Study sites

Research was done on intertidal cobble beaches of Narragansett Bay in Rhode Island, USA, a well-mixed estuary with semidiurnal tides ranging between 0.8–2 m. Two sites were used; Providence Point on Prudence Island (41°40' N, 71°20' W) and Haffenreffer Reserve (hereafter called Haffenreffer, 41°41' N, 71°14' W). Both sites support extensive cordgrass beds and abundant forb populations (Bruno 2000, Bruno and Kennedy 2000, Kennedy and Bruno 2000).

Does shoot density and height modify cordgrass facilitation of forbs?

Testing the hypothesis that forb abundance correlates with cordgrass shoot density and height was done in late June 2006 when cordgrass had completed much of its seasonal growth. At each site, the density and height of cordgrass shoots within 2 m of the upper margin of beds were sampled with haphazardly placed quadrats (0.2 × 0.2 m, n = 40 for density and an independent 40 for height). Forbs adjacent to each sampled patch of cordgrass (0.5–2 m away from the upper border) were then counted using larger quadrats (0.5 × 0.5 m) because of their lower densities and less uniform distribution relative to cordgrass (all values were converted to density/m² for analyses). Linear regression of untransformed data was used to examine the relationship of forb abundance with shoot density and height.

To experimentally test the hypothesis that cordgrass shoot density and height modify forb facilitation, shoot density within 10 patches of cordgrass was halved by manual thinning (termed “sparse,” ~250 shoots/m²), while another 10 patches were left at natural densities (“dense,” ~530 shoots/m²). Thinning cordgrass involved the “weeding out” of individual shoots and associated short roots, but rarely any attached peat, and was done evenly from the upper to lower border of the cordgrass bed and across a width of ~2 m (total area thinned ~10–16 m² per replicate), leaving unmanipulated cordgrass on either side. Shoots in five patches of each density treatment were then trimmed with shears to about half their natural height (“short,” ~30–40 cm), while the remaining patches in each density treatment were undisturbed (“tall,” ~75–90 cm; experimental
design, 2 density × 2 height × 5 replicates). Treatments were established only at Providence Point due to space restrictions at Haffenreffer, and were maintained every two weeks. Immediately behind each replicate, permanent quadrats (1 m²) were marked and the abundance of forbs within was quantified on haphazardly chosen days throughout the growing season.

Multiple species of forb were present but only one, *Suaeda linearis* (family Chenopodiaceae, commonly known as sea-blite), consistently occurred in great enough abundance for meaningful experimentation and analysis. Given the reliance of the entire forb community on the presence of cordgrass (Bruno 2000), other species may have shown similar responses to our experimental manipulations, but their abundances were too low to draw such conclusions with confidence. Experiments initially focused on *S. linearis* seedlings because their facilitation by cordgrass is the proximate life history stage limiting forb population size and distribution (Bruno 2000). However, most forbs in this system are annuals that depend on seed supply from prior seasons to maintain populations, and so experiments were repeated with adult *S. linearis* (using an independent set of cordgrass manipulations) and focused on survival and seed production. Experiments using seedlings began on 4 May and finished on 15 June (42 days), when *S. linearis* began a period of rapid growth into adults (*personal observations*). Experiments using adults began on 21 June and finished on 4 September (75 days) when seeds were present and early signs of senescence were visible (e.g., withering of leaves).

The percentage survival of *S. linearis* was calculated as the proportion of final to initial abundance, with analyses of arcsine-transformed data following two-way ANOVA and treating density and height as fixed and orthogonal factors. In addition, five individuals (repeated with adult *S. linearis*) were compared to uncut cordgrass ("shoots and peat") as well as to nearby "interbed" habitats at equivalent tidal heights. The experiment was repeated for *S. linearis* seedlings (May–June) and adults (June–Sept.), with survival, biomass, and seed production quantified as described above. Analyses were done with one-way ANOVA, with survival data arcsine transformed (Bonferroni-Holm adjustments also shown in Appendix B).

It is worth noting that while peat is certainly an integral component of cordgrass beds, we only tested the contribution of peat to the facilitation of forbs and not the role of variation in traits of peat (e.g., peat height or width) given the enormous logistical difficulties in creating such treatments. Also, the experimental clearance of shoots did not appear to affect cordgrass root biomass anchored within the peat because regrowth of shoots was rapid and constant, requiring the maintenance of treatments (removal of new shoot growth) on a weekly basis. As such, the "peat only" treatment can be considered a combination of primarily dead (peat) and living (roots) cordgrass biomass.

**Water flow and cobble stability measurements**

Since facilitation of forbs by cordgrass occurs through cordgrass buffering water flow and stabilizing cobbles, these variables were quantified in each experiment. Water flow was estimated from the dissolution of plaster blocks (Yund et al. 1991). Five replicate blocks were secured with epoxy on the surface of large stable cobbles in each treatment, ~0.5 m behind the upper margin of cordgrass (equivalent height for interbed treatments), and left for 9–12 days. Blocks were oven dried (70°C for 48 hours) before and after deployment, with change in mass used to calculate the percentage dissolved per day.

Cobble stability was quantified using the method of Bruno and Kennedy (2000). Small cobbles of similar size (~4 cm diameter) and shape (approximately round) were collected from study sites. In each experimental replicate, five individually numbered cobbles were placed at regular distances on a transect ~0.5 m above the upper margin of cordgrass. These cobbles were located the following day (after two tidal cycles) and the linear distance each had moved was measured. The mean distance of the five cobbles within each replicate was used as a single replicate for statistical analyses.

**RESULTS**

*Does shoot density and height modify cordgrass facilitation of forbs?*

Forb abundance correlated positively with cordgrass shoot density and height (Fig. 1a, b). Similar relation-
ships were observed between sites, so data were combined for final analysis. Variation in shoot density explained 44% of the intrabed variation in forb abundance, while shoot height explained 29%.

Manipulating cordgrass shoot density and height significantly affected S. linearis survival (Table 1). Dense cordgrass maintained seedling survival at 100%, while sparse cordgrass reduced survival to 76% when tall, or 40% when short (Fig. 2a; Table 1, density main effect; SNK tests, dense = tall, sparse = short). Survival of adults was 35% greater behind dense cordgrass, and was unaffected by height manipulations (Fig. 2b; Table 1, density main effect; SNK tests, dense > sparse).

Thinning cordgrass also reduced seedling and adult biomass by up to 82% and 63% respectively (Fig. 3a, b; ANOVA density main effect, F_{1,16} = 27.31, P = 0.0001 for seedling biomass, F_{1,16} = 7.28, P = 0.0158 for adult biomass), and reduced seed production by as much as 57% (Fig. 3c; ANOVA density main effect, F_{1,16} = 4.70, P = 0.0455). Manipulating cordgrass height only affected seedlings behind sparse cordgrass, further

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**Table 1.** Results of two-way ANOVAs testing the effects of cordgrass shoot density (dense vs. sparse) and height (tall vs. short) on the survival of S. linearis seedlings and adults.

<table>
<thead>
<tr>
<th>Stage and source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seedling</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>density</td>
<td>1</td>
<td>8149.80</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>height</td>
<td>1</td>
<td>2252.27</td>
<td>13.41</td>
<td>0.0021</td>
</tr>
<tr>
<td>density x height</td>
<td>1</td>
<td>1051.74</td>
<td>6.26</td>
<td>0.0235</td>
</tr>
<tr>
<td>residual</td>
<td>16</td>
<td>167.96</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>density</td>
<td>1</td>
<td>6026.87</td>
<td>19.97</td>
<td>0.0004</td>
</tr>
<tr>
<td>height</td>
<td>1</td>
<td>318.87</td>
<td>1.06</td>
<td>0.3193</td>
</tr>
<tr>
<td>density x height</td>
<td>1</td>
<td>6.09</td>
<td>0.02</td>
<td>0.8888</td>
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<tr>
<td>residual</td>
<td>16</td>
<td>301.76</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Notes:** Significant results are shown in boldface type. The data analyzed are for the final day of sampling. All data were arcsine transformed prior to analysis. Cochran’s C test of homogeneity of variances: P > 0.05 for each test.
reducing biomass by 72% when cordgrass was short (Fig. 3a; ANOVA density × height interaction, $F_{1,16} = 4.98$, $P = 0.0403$; SNK tests, dense and tall = dense and short > sparse and tall > sparse and short).

Does peat facilitate forb success?

Removing cordgrass shoots showed that the peat base still had a substantial positive effect on forbs. Similar responses occurred between sites, so data were combined for final analysis. Survival of *S. linearis* seedlings was greatest where shoots remained intact (~110%, more *S. linearis* emerged after the experiment was established), yet survival where shoots were removed was still reasonable at ~62%, and certainly distinct from nearby interbed regions where no forbs were found (Fig. 4a; ANOVA on final day across sites, $F_{2,27} = 27.55$, $P < 0.0001$; SNK tests, shoots and peat > peat only > interbed). Removing cordgrass shoots did not influence adult *S. linearis*, with survival in the presence and absence of shoots sampled at ~52–66% across sites (Fig. 4b; ANOVA on final day, $F_{2,27} = 27.61$, $P < 0.0001$; SNK tests, shoots and peat = peat only > interbed).
At both sites, removing cordgrass shoots reduced per capita *S. linearis* seedling biomass by ~60%, adult biomass by 66%, and seed production by 65% (Table 2; ANOVA, $F_{1,18} = 38.44, P < 0.0001$ for seedling biomass; $F_{1,18} = 40.60, P < 0.0001$ for adult biomass; and $F_{1,18} = 18.18, P = 0.0005$ for seed production).

**Table 2.** A summary of the experimental effects of cordgrass shoot removal on *S. linearis* seedling biomass, adult biomass, and number of seeds produced.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Shoots and peat</th>
<th>Peat only</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seedling biomass (g dry mass)</td>
<td>0.180 ± 0.014</td>
<td>0.071 ± 0.011</td>
</tr>
<tr>
<td>Adult biomass (g dry mass)</td>
<td>4.519 ± 0.366</td>
<td>1.526 ± 0.294</td>
</tr>
<tr>
<td>Number of seeds per plant</td>
<td>465.90 ± 56.52</td>
<td>163.44 ± 42.86</td>
</tr>
</tbody>
</table>

*Note:* Values shown are means ± SE.

Water flow and cobble stability measurements

For the test of cordgrass density and height, water flow increased behind sparse cordgrass (25–32% greater dissolution of plaster; ANOVA, density effect, $F_{1,16} = 50.92, P < 0.0001$), but was unaffected by cordgrass height (ANOVA, height effect, $F_{1,16} = 3.74, P = 0.0709$). Cobble movement was negligible in this experiment (0.08–0.36 cm of movement), and did not statistically differ among treatments (the greatest likelihood of statistical significance was for density; ANOVA, $F_{1,16} = 3.18, P = 0.0933$). However, both water flow and cobble movement ranked as greater behind short cordgrass (see Appendix C), and may therefore still explain the observed effect of height on *S. linearis* seedlings (Figs. 2a and 3a).

For tests of peat contribution, water flow was greatest in interbed habitats (57–65% dissolution of plaster), less behind peat (53%), and even less behind cordgrass shoots (47–49%; ANOVA, $F_{2,15} = 23.76, P < 0.0001$ at Providence Point; $F_{2,15} = 112.48, P < 0.0001$ at Haffenriffer; SNK tests, shoots and peat < peat only < interbed at both sites). Cobble movement was negligible whether cordgrass shoots were removed or not (0.3–1.6 cm of movement) but increased to 6.2–11.8 cm in interbed habitats (ANOVA, $F_{2,12} = 10.58, P = 0.0022$ at Providence Point; $F_{2,12} = 4.72, P = 0.0308$ at Haffenriffer; SNK tests, shoots and peat = peat only < interbed at both sites).

**Discussion**

Facilitation as a process affecting the distribution and abundance of plants and animals was considered a century ago (Clements 1916), but has only recently received attention from researchers. Consequently, there are many questions about facilitation and its importance relative to the better studied processes of competition and predation. Among these, understanding how traits of a foundation species modify its positive effects on associated species is key, since the very occurrence of facilitation may depend on specific traits (Bruno and Kennedy 2000). Using cobble beach cordgrass beds, a habitat known to facilitate both terrestrial plant and marine invertebrate communities (Bruno 2000, Altieri et al. 2007), we have shown that the population-level traits of cordgrass shoot density and height modify its facilitative properties.

Foundation species such as trees, grasses, seagrasses, and kelps often form extensive habitats but vary substantially at smaller (patch) scales in traits such as density and height. On cobble beaches, forb abundance correlated positively with cordgrass shoot density and height (Fig. 1a, b), and experimental manipulation of these two traits demonstrated consistently strong effects of shoot density on forb survival, biomass, and seed production. Effects of shoot height were comparatively minor, suggesting that cordgrass shoot density plays a greater facilitative role than shoot height over the life cycle of forbs.

In other habitats, population density is an important structural feature that can affect the abundance of associated species. For example, the density of fish can be positively related to the density of plants within subtidal forests of macroalgae (e.g., kelps; Anderson 1994, Levin and Hay 1996). In seagrass beds, fish and shrimp density can increase with plant density (Fonseca et al. 1996), possibly because greater densities of seagrass shoots offer greater protection from predators (Orth et al. 1984). Density is even important for maintaining species richness and abundance of soft-sediment infauna within habitats created by tube-building polychaetes (Woodin 1978). Collectively, these results suggest that density may be a key and general population-level trait that can modify facilitation by many foundation species.

There may also be some generalities in the mechanism(s) by which density modifies facilitation. In this study, water flow and cobble movement were least behind dense cordgrass, agreeing with previous studies (Gleason et al. 1979, Leonard and Luther 1995), and suggesting that cordgrass density modifies facilitation of forbs through the primary mechanism identified by Bruno (2000; i.e., reduced flow and stabilized cobbles). Reduced flow at increased densities occurs among other aquatic foundation species, such as kelp forests (Eckman et al. 1989) and seagrass beds (Eckman 1987), and can affect the type and abundances of species facilitated (Eckman 1987, Grizzle et al. 1996) as well as the physiology and recruitment of the facilitator (Dennison and Barnes 1988, Eckman et al. 1989). Analogous
examples can be found for wind in terrestrial forests (Jones et al. 1994). As noted above, greater plant densities can also inhibit predator/herbivore foraging and thereby provide a refuge from consumption for prey (Crowder and Cooper 1982, Orth et al. 1984), though such effects appear irrelevant for cordgrass–forb facilitation because herbivory appears negligible in this system (Bruno 2000, Kennedy and Bruno 2000). The consequences to facilitation of other factors commonly affected by density (e.g., temperature, light intensity, desiccation stress; Bertness et al. 1999) are largely unknown.

In addition to the influence of cordgrass shoots, we found that the peat base makes a substantial contribution to forb facilitation across the growing season. Removing shoots to leave only peat did not reduce forb seedling survivorship to zero as is characteristic of nearby interbed habitats, but instead maintained the strength of facilitation at \(\sim 40\% \) of treatments where shoots remained intact (Fig. 4). Bruno and Kennedy (2000) previously suggested that peat and shoots act synergistically to reduce physical disturbance and enhance facilitation of forbs. While our experiment was not designed to detect this synergy, as such an experiment would require orthogonal combinations of the presence and absence of cordgrass shoots and peat, our results nevertheless show that the peat itself plays a role in the cordgrass–forb facilitation. Since cordgrass beds are primarily peat when forbs emerge (March–April), peat may be particularly important for facilitating forb establishment before cordgrass shoots can grow and further ameliorate stress. Indeed, sampling of forb seedling emergence revealed that substantial cordgrass shoot biomass is not a prerequisite (see Appendix D).

For any foundation species, numerous traits are likely to influence facilitation. As such, it may be possible to predict the strength of facilitation in a hierarchical fashion whereby successive trait thresholds are reached. Using the current example, a cordgrass bed at least 25 m long appears to be a primary trait threshold for forb facilitation since the area behind smaller beds generally remains unoccupied because small beds do not sufficiently ameliorate environmental stress (Bruno and Kennedy 2000, Bruno 2002). Within these larger beds, if cordgrass shoots are dense (\(\sim 530\) shoots per m\(^2\)) then forb facilitation is strengthened. However, if cordgrass is
sparse (~250 shoots/m²), forb facilitation may be enhanced behind tall cordgrass (~75–90 cm), but not behind short cordgrass (~30–40 cm; Figs. 2 and 3). With more research, other traits such as bed orientation, width, and peat height could also be included. We expect that similar predictive hierarchies exist for other systems structured by foundation species.

Foundation species vary in their expression of traits, ensuring that the amount of habitat/resources provided and the degree of environmental modification varies substantially over multiple scales of space and time. In short, not all foundation species, or even patches of a single foundation species, are created equal. This understanding can help us predict where and when facilitation may be strong or weak, but is also important for developing conservation strategies. It has been argued that protecting foundation species as habitat is a better strategy for maximizing preservation of biodiversity than individually targeting the inhabiting species, but merely protecting a foundation species is not adequate if threshold levels of particular traits must be met (Bruno and Bertness 2001). For example, efforts to restore salt marsh using short-form cordgrass failed to attract the conservation target species, endangered Light-footed Clapper Rails, because they prefer tall-form cordgrass (Malakoff 1998). Clearly, understanding the role of traits for facilitation can increase the likelihood of success for important but expensive and time-consuming conservation efforts.

Facilitation through habitat provision and environmental modification is a fundamental process affecting the distribution, abundance, and diversity of life, yet there is still much to learn because ecologists have only recently become interested in positive species interactions (Bruno and Bertness 2001, Grutter and Irving 2007). For a comparatively well-understood interaction (cordgrass–forb facilitation), we have shown how variation in two common population-level traits of foundation species can substantially modify its capacity to facilitate. Such information not only builds upon our theoretical understanding of facilitation as an ecological process, but also highlights that the strength or even occurrence of facilitation cannot be assumed just because a foundation species is present. Further work will likely identify cross-system consistencies that lend themselves to the development of general ecological theories that explain spatial and temporal variation in facilitation, and the resulting effects on population dynamics and community structure.

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APPENDIX A

A color version of Plate 1, showing a typical cobble beach plant community (Ecological Archives E090-218-A1).

APPENDIX B

Bonferroni-Holm adjustments (Ecological Archives E090-218-A2).

APPENDIX C

Effects of cordgrass shoot density and height on water flow and cobble movement (Ecological Archives E090-218-A3).

APPENDIX D

Patterns in the emergence of cordgrass and forbs on cobble beaches (Ecological Archives E090-218-A4).