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# Facilitative and competitive interaction components among New England salt marsh plants

John F Bruno <sup>Corresp., 1</sup>, Tatyana A Rand <sup>2</sup>, Nancy C Emery <sup>3</sup>, Mark D Bertness <sup>4</sup>

<sup>1</sup> Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, United States

<sup>2</sup> Northern Plains Agricultural Research Laboratory, USDA-ARS, Sidney, MT, USA

<sup>3</sup> Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO, United States

<sup>4</sup> Department of Ecology and Evolutionary Biology, Brown University, Providence, RI, United States

Corresponding Author: John F Bruno

Email address: jbruno@unc.edu

Intra- and interspecific interactions can be broken down into facilitative and competitive components. The net interaction between two organisms is simply the sum of these counteracting elements. Disentangling the positive and negative components of species interactions is a critical step in advancing our understanding of how the interaction between organisms shift along physical and biotic gradients, and whether component interactions are unique or redundant across species in natural communities. We performed a manipulative field experiment to quantify the positive and negative components of the interactions between a perennial forb, *Aster tenuifolius*, and three dominant, matrix-forming grasses and rushes in a New England salt marsh. Specifically, we asked whether positive and negative interaction components: (1) are unique or redundant across three matrix-forming grass and rush species (*Juncus gerardi*, *Distichlis spicata*, and *Spartina patens*), and (2) change across *Aster* life stages (seedling, juvenile, and adult). For adult forbs, the strength of the facilitative component of the matrix-forb interaction was stronger than the competitive component for two of the three matrix species, leading to net positive interactions. There was no statistically significant variation among matrix species in their net or component effects, however, the competitive effect of *J. gerardi* was negligible, especially compared to that of *D. spicata*. We found little difference in the effects of *J. gerardi* on *Aster* at later life-history stages; interaction component strengths did not differ between juveniles and adults. However, mortality of seedlings in neighbor removal plots was 100%, indicating a particularly strong and critical facilitative effect of matrix species on this forb during the earliest life stages. Overall, our results indicate that matrix forming grasses and rushes have important, yet largely redundant, positive net effects on *Aster* performance across its life cycle. Studies that untangle various components of interactions and their contingencies are critical to both expanding our basic understanding of community organization, and predicting how natural communities and

their component parts will respond to environmental change.

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## 2 **Facilitative and competitive interaction components among New England salt** 3 **marsh plants**

4

5 John F. Bruno<sup>1,2</sup>, Tatyana A. Rand<sup>3</sup>, Nancy C. Emery<sup>4</sup>, and Mark D. Bertness<sup>5</sup>

6

7 <sup>1</sup>corresponding author8 <sup>2</sup>Department of Biology, The University of North Carolina, Chapel Hill, NC, USA 27599-3280

9

10 <sup>3</sup>USDA-ARS Northern Plains Agricultural Research Laboratory, 1500 North Central Ave,  
11 Sidney, MT, USA

12

13 <sup>4</sup>Department of Ecology and Evolutionary Biology, Box 0334, University of Colorado Boulder,  
14 Boulder, CO, USA

15

16 <sup>5</sup>Department of Ecology and Evolutionary Biology, Brown University, Providence, RI, USA

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20 **Abstract:** Intra- and interspecific interactions can be broken down into facilitative and  
21 competitive components. The net interaction between two organisms is simply the sum of these  
22 counteracting elements. Disentangling the positive and negative components of species  
23 interactions is a critical step in advancing our understanding of how the interaction between  
24 organisms shift along physical and biotic gradients, and whether component interactions are  
25 unique or redundant across species in natural communities. We performed a manipulative field

26 experiment to quantify the positive and negative components of the interactions between a  
27 perennial forb, *Aster tenuifolius*, and three dominant, matrix-forming grasses and rushes in a  
28 New England salt marsh. Specifically, we asked whether positive and negative interaction  
29 components: (1) are unique or redundant across three matrix-forming grass and rush species  
30 (*Juncus gerardi*, *Distichlis spicata*, and *Spartina patens*), and (2) change across *Aster* life stages  
31 (seedling, juvenile, and adult). For adult forbs, the strength of the facilitative component of the  
32 matrix-forb interaction was stronger than the competitive component for two of the three matrix  
33 species, leading to net positive interactions. There was no statistically significant variation  
34 among matrix species in their net or component effects, however, the competitive effect of *J.*  
35 *gerardi* was negligible, especially compared to that of *D. spicata*. We found little difference in  
36 the effects of *J. gerardi* on *Aster* at later life-history stages; interaction component strengths did  
37 not differ between juveniles and adults. However, mortality of seedlings in neighbor removal  
38 plots was 100%, indicating a particularly strong and critical facilitative effect of matrix species  
39 on this forb during the earliest life stages. Overall, our results indicate that matrix forming  
40 grasses and rushes have important, yet largely redundant, positive net effects  
41 on *Aster* performance across its life cycle. Studies that untangle various components of  
42 interactions and their contingencies are critical to both expanding our basic understanding of  
43 community organization, and predicting how natural communities and their component parts will  
44 respond to environmental change.

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## 49 INTRODUCTION

50 Research on the importance of facilitation in community organization has recognized that species  
51 interactions are often composed of both negative (competitive) and positive (facilitative)  
52 components (Callaway 1994, Greenlee and Callaway 1996, Callaway and Walker 1997, Claus  
53 Holzapfel and Mahall 1999, Stachowicz 2001). The relative importance of these components is  
54 likely to shift along gradients of physical stress and consumer pressure. For example,  
55 competition between common acorn barnacles for space in rocky intertidal habitats (Connell  
56 1961) is a classic illustration of the role played by competition in determining fine-scale  
57 distribution patterns within natural communities. But at high tidal heights (Bertness 1989,  
58 Bertness et al. 1999a) and in warmer climates (Lively and Raimondi 1987, Bertness et al. 1999b,  
59 Leonard 2000), barnacle neighbors actually facilitate one another by buffering against  
60 desiccation stress. Examples from desert (Muller 1953, Niering et al. 1963), chaparral (Callaway  
61 et al. 1991), and salt marshes (Bertness and Hacker 1994, Callaway 1994) illustrate that plant  
62 interactions also commonly shift from competitive to facilitative across physical stress gradients.  
63 This does not trivialize the role played by competition in natural communities; instead, it  
64 improves our understanding of when and under what conditions competitive forces play  
65 dominant roles in structuring communities.

66 Our current knowledge of the balance between the positive and negative components of  
67 species interactions is limited. One specific issue that needs further exploration is how this  
68 balance changes ontogenetically across the life history stages of the interacting organisms to  
69 determine the net effect of each species on the other. In many plants (Muller 1953, Niering et al.  
70 1963, Callaway 1994, Bruno and Kennedy 2000, Rand 2000, Yelenik et al. 2015) and sessile  
71 invertebrates (Dayton 1975, Bertness and Grosholz 1985, Leonard 1999), recruits and juveniles

72 depend on neighbors for early survival and growth, but as adults they may primarily compete  
73 with these same neighbors (Niering et al. 1963, Bertness and Grosholz 1985, Bertness and Yeh  
74 1994, Callaway 1995). In this situation, common in stressful environments, facilitation of  
75 juveniles may establish clumped adult distribution patterns that are dominated by competitive  
76 forces. In other cases, the situation is reversed: for example, a number of studies have found  
77 stronger competitive effects at early life history stages (emergence or recruitment), with  
78 interactions becoming neutral to facilitative at later life history stages (adult survival) (Thomson  
79 2005, Leger and Espeland 2010, Rojas-Sandoval and Meléndez-Ackerman 2012). Additionally,  
80 whether interactions are predominately competitive or facilitative at a given life stage can  
81 depend strongly on the environmental context (Rand et al. 2015).

82 More generally, we still know very little about how positive and negative interaction  
83 component strengths vary among species. Is species identity an important consideration or are  
84 species redundant in the positive and negative effects they exert on their neighbors and the  
85 community as a whole? The answer to this question is likely to depend on the specific  
86 mechanisms by which competition and/or facilitation operates among species, which is in turn  
87 likely to vary depending on the study system examined. For example, the effect of nurse shrubs  
88 on seedling survival and growth in Mediterranean environments have been shown to depend  
89 strongly on shrub identity, suggesting a lack of functional redundancy among facilitators  
90 (Gómez-Aparico et al. 2004). In contrast, two sea grass species were found to have broadly  
91 similar (i.e. redundant) effects on the composition of associated fouling communities (Moore and  
92 Duffy 2016).

93 In salt marsh plant communities, positive interactions are strongly driven by neighbors  
94 shading one another from physical stress (Bertness and Yeh 1994), in which case

95 morphologically similar species might be predicted to have similar positive effects on neighbors.  
96 However, the competitive components of these neighbor interactions will depend on the  
97 resources being competed for and the morphological and physiological adaptations of the  
98 competing species. Thus, in salt marshes, the positive components of species interactions may  
99 be redundant, while the competitive components may not, lead to a de-coupling of the  
100 components.

101 To date, experiments separating interaction components have only been performed in a  
102 few systems (Greenlee and Callaway 1996, Claus Holzapfel and Mahall 1999), and to our  
103 knowledge no studies have examined how interaction components shift ontogenetically across  
104 the life history of the species or with the identity of organisms in the same functional group. The  
105 purpose of this study was to answer two questions related to the context-dependency of species  
106 interaction components: (1) Do the strength of the positive and negative components of the  
107 interaction between a perennial salt marsh forb, *Aster tenuifolius*, and matrix forming grasses and  
108 rushes, change with the identity of the matrix species (*Juncus gerardi*, *Distichlis spicata*, and  
109 *Spartina patens*)?, and (2) Does the strength of these components vary with life stage of *A.*  
110 *tenuifolius* (seedling, juvenile, and adult)?

111

## 112 METHODS

113 **Study system:** We conducted a field experiment at Nag Creek marsh on Prudence Island, Rhode  
114 Island, USA, to examine the components of interactions among plant species in a southern New  
115 England salt marsh system. Nag Creek is typical of New England salt marshes, which are  
116 characterized by dense stands of perennial grasses and rushes which form bands, or zones, across  
117 the tidal gradient (Niering and Warren 1980, Nixon 1982, Bertness and Ellison 1987). Variation

118 in the frequency of flooding results in a strong gradient in salinity and soil oxygen availability  
119 (redox potential) corresponding to tidal height (Bertness and Hacker 1994, Hacker and Bertness  
120 1999). The seaward marsh zone is dominated by the grass *Spartina alterniflora*, which is  
121 replaced by *Spartina patens* and then a rush, *Juncus gerardi*, with increasing elevation and  
122 distance from the shoreline. Another grass, *Distichlis spicata*, is patchily distributed within the *S.*  
123 *patens* and *J. gerardi* zones (Miller and Egler 1950, Bertness and Ellison 1987). This species is  
124 generally abundant only in areas of high disturbance or increased physiological stress, where  
125 competition with the zonal dominants is absent (Brewer and Bertness 1996).

126       A group of less abundant halophytic forbs (herbaceous dicots) are generally found  
127 interspersed within the matrix of dominant grasses and rushes. Many of these forbs experience  
128 strong competitive suppression by the dominant matrix species which can limit both seedling  
129 recruitment and adult plant survival and reproduction (Ellison 1987, Shumway and Bertness  
130 1992, Brewer et al. 1998, Rand 2000). Under stressful conditions, however, these same grasses  
131 and rushes ameliorate soil conditions and have a net facilitative effect on forbs (Bertness and  
132 Shumway 1993, Bertness and Hacker 1994). Facilitation results primarily from shading of the  
133 substrate by the vegetation canopy which reduces surface evaporation and the accumulation of  
134 salt on the soil surface (Bertness et al. 1992, Callaway 1994), but possibly also by oxygenation  
135 of the soil (Bertness 1991). The degree to which different matrix marsh species vary in their  
136 competitive or facilitative effects on salt marsh forbs is not known, in part because earlier work  
137 has been done within natural zone communities and did not differentiate between effects of  
138 neighbor identity and tidal elevation (Hacker and Bertness 1999, Rand 2000). In addition, while  
139 previous studies have examined the net effects of matrix species on forbs, the relative strengths

140 of the competitive and facilitative components of the grass-forb interaction have not been  
141 quantified in this system.

142 Our experimental target species was *Aster tenuifolius* (Asteraceae), a relatively salt-  
143 tolerant perennial that germinates in early spring, flowers in late fall, and produces small wind-  
144 dispersed seeds following reproduction. This species is abundant in both the *S. patens* and *J.*  
145 *gerardi* zones in New England salt marshes and is also frequently found in association with *D.*  
146 *spicata*. (Brewer et al. 1998, Rand 2000). We manipulated the species identity and structure of  
147 the matrix vegetation surrounding seedling, juvenile, and adult *Aster* plants to test if the  
148 facilitative, competitive, and net interaction effects on *Aster* are affected by neighboring plant  
149 identity, neighboring plant density, or the life stage of *Aster* individuals. We were specifically  
150 interested in the unidirectional effects of matrix species on marsh forbs, such as *Aster*, and not  
151 the reciprocal effects.

152 **Experimental design:** Our experimental design included three treatments, with individual  
153 replicates of each treatment clustered spatially into blocks within each matrix species: (1) an  
154 unmanipulated control, (2) a neighbor removal, and (3) a facilitation mimic that duplicates the  
155 positive effects of the neighbor without any of the negative effects (Fig. 1). In control treatments,  
156 vegetation was left intact. In vegetation removal treatments all above ground vegetation within  
157 the 0.25m<sup>2</sup> plot was clipped at the substrate surface with scissors once every two weeks until  
158 regrowth no longer occurred. In facilitation mimic treatments, all above ground vegetation was  
159 once again removed to eliminate competition for light. Plots were then covered with 0.25 m<sup>2</sup>  
160 pieces of shade-cloth that were pinned to the substrate surface using plastic staples. Shade-cloth  
161 reduces soil surface evaporation to effectively mimic the facilitating effects of plant neighbors

162 (Bertness et al. 1992). Shade-cloth was spray-painted white to avoid soil temperature increases  
163 that often occur under black cloth in the field.

164 We manipulated the identity of the matrix species, while controlling for environmental  
165 context, by transplanting square plots (0.25 m<sup>2</sup> in area, 50 cm deep) of the three matrix species  
166 (*S. patens*, *J. gerardi*, and *D. spicata*) into the *J. gerardi* (high marsh) zone in the Nag Creek  
167 marsh during the winter of 1999. Transplanting all matrix species into a single marsh zone  
168 allowed us to standardize tidal height so that any differences between species could be attributed  
169 directly to neighbor identity. Thirty *Spartina patens* and *D. spicata* plots were removed and  
170 placed into equal-sized holes in the *J. gerardi* zone. *J. gerardi* plots were lifted out of the soil  
171 and then replaced to simulate transplantation. Transplanted plots were grouped into ten blocks  
172 with three plots/block for *D. spicata* and *S. patens* matrix transplants and the *J. gerardi* plots  
173 used for *Aster* seedlings and juvenile plants (10 blocks for each). For the *J. gerardi* - adult *Aster*  
174 plots (20 blocks), we included an additional fourth treatment in each block: a thinning treatment  
175 in which vegetation was thinned to 50% of its original density by clipping with scissors.

176 In mid-May of 1999, after the transplanted matrix plots had established in their new  
177 locations and experimental treatments were in place, *Aster* individuals were collected from  
178 natural populations at Nag Creek and a single target adult plant (>2 true leaves) was transplanted  
179 into the center of each plot of each matrix species. Seedlings were identified by the presence of  
180 cotyledons, and juvenile plants were one-year-old, pre-reproductive individuals with < 2 true  
181 leaves and no cotyledons present. The mean ( $\pm$  1 SE) height (cm) and dry weight (mg) of the  
182 three experimental life stages (n = 100) were as follows: seedling height =  $0.72 \pm 0.07$ , seedling  
183 weight =  $1.64 \pm 0.12$ ; juvenile height =  $6.49 \pm 0.21$ , juvenile weight =  $24.97 \pm 1.58$ ; adult height  
184 =  $16.61 \pm 0.44$ , adult weight =  $146.45 \pm 5.27$ . In the vegetation mimic treatments, *Aster*

185 transplants were inserted through a slit that was made in the center of the shade-cloth, and the  
186 cloth was then pinned back together around the stem using plastic staples. All *Aster* transplants  
187 were watered for the first week after planting to minimize transplant shock, and plants that died  
188 within the first two weeks after transplantation were replaced. The experiment was set up by  
189 June 1, 1999 and was harvested in August 1999.

190 Salinity and light levels were quantified in each plot on July 20 and August 20, 1999, to  
191 evaluate the effects of the experimental treatments on potential salt stressors and above-ground  
192 competition. Salinity measurements were taken by extracting a core of peat, 3 cm diameter x 3  
193 cm deep, in each matrix plot. We pressed each sample through cotton gauze cloth and quantified  
194 salinity of the extracted pore water using a hand-held NaCl refractometer (precision =  $\pm 1 \text{ g kg}^{-1}$ ).  
195 Light levels were measured between 10:00 AM and 2:00 PM with a LiCor solar monitor (Model  
196 1776). Instantaneous measurements ( $\mu\text{E m}^{-2} \text{ s}^{-1}$ ) were taken 5 cm above the soil surface (the  
197 height of the sensor) and above the canopy in each experimental plot. To estimate the initial  
198 mass of *Aster* transplants, we measured the longest leaf length of each experimental *Aster* on  
199 June 17, 1999. Longest leaf length was also measured on an additional 82 juvenile and 43 adult  
200 *Aster* individuals that were then harvested and weighed the same month. A regression equation  
201 between longest leaf length and biomass was used to estimate initial biomass of experimental  
202 plants (adults:  $y = 0.04039 x - 0.13501$ , adjusted  $R^2 = 0.77$ ; juveniles:  $y = 0.01433 x - 0.02160$ ,  
203 adjusted  $R^2 = 0.76$ ). Final biomass was estimated by harvesting all experimental plants at the end  
204 of August, drying them to a constant mass into a drying oven at  $55^\circ\text{C}$  for one week, and  
205 weighing each plant to the nearest milligram. Relative growth was calculated for each plant as:  
206 (measured final biomass – predicted initial biomass) / predicted initial biomass.

207 We used three simple equations to calculate the positive and negative components within  
208 each block:

209 strength of positive component = mimic – removal

210 strength of negative component = control – mimic

211 strength of net component = control – removal

212 Interaction strength components were calculated using both final mass and relative growth. We  
213 compared the absolute value of each interaction component among matrix species and *Aster* life  
214 stages with one-factor ANOVA (block was not included as a treatment since each block  
215 produces a single value for each interaction type).

216

## 217 **RESULTS**

218 There was little variance in light reduction across the three matrix species (Fig. 2). The  
219 experimental treatments manipulated light and salinity levels as intended. The matrix vegetation  
220 reduced light at the soil surface to just less than 20% ambient, and thinning *J. gerardi* roughly  
221 doubled the amount of available light to ~40% ambient (Fig. 2). Vegetation removal resulted in a  
222 substantial increase in salinity levels from a mean of 46.8 g kg<sup>-1</sup> (± 1.3, SE) in mimic and  
223 vegetation treatments to 71.3 g kg<sup>-1</sup> (± 2.2) in vegetation removal treatments (Fig. 2). Thinning  
224 of the *J. gerardi* canopy had no significant effect on salinity and the full canopy of all three  
225 matrix species reduced salinity to similar levels (Fig. 2). Vegetation mimics were effective in  
226 increasing light transmittance to levels similar to those in removal treatments while maintaining  
227 salinity at levels similar to those within natural vegetation (Fig. 2), suggesting this treatment  
228 effectively replicated the salinity reduction aspect of facilitative interaction component.

229           Due to mortality of some of the experimental *Aster* transplants, our sample size was  
230 reduced to 9 for juvenile *Aster* (in *J. gerardi*), 8 for adult *Aster* in *S. patens*, and 14 for adult  
231 *Aster* in *J. gerardi*. None of the *Aster* transplants in *D. spicata* were lost. Mortality of *Aster*  
232 seedlings in the matrix removal treatments was 100%, 0% in the vegetation (“Intact”) plots, and  
233 58% in the facilitation mimic plots, hence seedling data could not be used in the primary  
234 analysis, i.e., we could not calculate interaction component strengths for the seedling stage.  
235 Initial adult *Aster* biomass, estimated from regression equations (described above), did not differ  
236 between the three matrix species, or between neighbor manipulation treatments (Fig. 2). By the  
237 end of the experiment growth varied significantly between treatments (Fig. 3). Regardless of the  
238 matrix species, the strength of the positive component of the matrix-forb interaction outweighed  
239 the negative component, resulting in a positive net effect of the matrix species on *Aster* adults  
240 and juveniles (Fig 4). There was no significant variation among matrix species in their net effects  
241 or interaction components, however, the negative effect of *J. gerardi* appeared negligible  
242 compared to that of *D. spicata* (Fig. 4). Calculation of interaction component strengths based on  
243 final mass and relative growth (Fig. S1) were qualitatively similar. Within the *J. gerardi* matrix,  
244 relative growth of adult and juvenile *Aster* was lower in removal treatments than in mimic,  
245 thinned, and control (intact vegetation) treatments, and did not differ significantly among the  
246 later three treatments (Fig. 3). The effects *J. gerardi* neighbors did not vary among *Aster* juveniles  
247 and adults.

248

## 249 **DISCUSSION**

250 Our results indicate that the net effect of matrix species on forbs consists of both positive and  
251 negative components, the strength of which did not differ significantly among matrix species or

252 later *Aster* life stages. The strength of the positive component was generally stronger than the  
253 negative component (except for *D. spicata*) resulting in a positive net effect of the matrix species  
254 on *Aster*. Previous studies have defined *J. gerardi* to be the “keystone facilitator” in this system  
255 (Hacker and Gaines 1997). The strength of the facilitative component was as strong for *D.*  
256 *spicata* and *S. patens* as it was for *J. gerardi*, suggesting that other matrix species can play a  
257 similar functional role as *J. gerardi*.

258         Thinning *J. gerardi* blades by 50% significantly increased light availability to *Aster*  
259 transplants but had no effect on salinity levels or *Aster* growth rates. Adult *Aster* growth in the  
260 thinning plots was similar to growth in intact vegetation. The relatively weak (but not  
261 significantly different) competitive effect of *J. gerardi* may in part be explained by the fact that it  
262 grows and flowers earlier than the two grass species, and then dies back relatively early in the  
263 growing season. This could reduce competition with forbs later in the summertime. Moreover,  
264 the blades of *J. gerardi* tend to decompose rapidly, thus it does not form the dense thatch of  
265 standing dead, which is characteristic of both *S. patens* and *D. spicata* canopies. These traits  
266 could reduce the strength of the positive and negative effects of *J. gerardi* on its neighbors. In  
267 any case, the fact that *S. patens*, *J. gerardi*, and *D. spicata* reduce salinity to similar levels and  
268 positively affect *Aster* growth to a similar degree suggests that all three species serve a strong  
269 facilitative function in New England salt marshes. Thus, in this system the role of matrix species  
270 as facilitators appears to be largely redundant. This is consistent with the hypothesis that species  
271 from the same functional group have similar effects on other functional types within the same  
272 community; however, we expect that other functional groups, such as forbs or shrubs, are likely  
273 to have different net effects (and relative contributions of competitive and facilitative  
274 components).

275           The interpretation of our experiment assumes that all grass and rush matrix species share  
276 a common mechanism of facilitation of marsh forbs – the reduction of soil salinity by shading  
277 the substrate. However, some marsh matrix species also aerate the soil and hide neighbors from  
278 herbivores (Ellison 1987, Hacker and Bertness 1999), which could serve as other mechanisms  
279 for enhanced forb fitness. The same is true in many cases of plant-plant competition because  
280 neighboring individuals are often simultaneously competing for multiple resources (e.g. light,  
281 water, nutrients, and even space in one sense). Including more than one facilitation or  
282 competition mimic treatment to simulate the effects of other facilitative or competitive  
283 mechanisms could be used to tease apart the strength and context specificity of each individual  
284 mechanism. On the other hand, if the main interest is to determine the cumulative effect of all  
285 facilitative or competitive mechanisms, the interaction mimics will have to be designed to  
286 include all known mechanisms.

287           We found little difference in the effects of matrix species on the performance of *Aster* at  
288 different life history stages. For example, there were no differences between either raw growth  
289 rates or interaction component strengths between juvenile and adult *Aster*. Mortality of seedlings  
290 in *J. gerardi* removal plots was 100%, and thus interaction component strengths could not be  
291 calculated for this life stage. However, the high mortality clearly indicates that there is a strong  
292 and critical facilitative effect of matrix species on this forb during the earliest life stages, a  
293 finding concordant with other empirical studies (e.g. Kennedy and Bruno 2000). One of the  
294 largest drawbacks of our experiment was the high within-treatment variance that reduced our  
295 power to detect differences among treatments. Statistical power could be improved by increasing  
296 the sample size, however, under conditions where mortality of individuals may be exceedingly  
297 high, as found for the seedling life stage in the present study, we suggest that within-treatment

298 variability could be reduced by setting up replicate response individuals (here, *Aster* transplants)  
299 in each plot. For individual-level response variables like growth or fecundity, a plot-wide mean  
300 could be calculated. This approach would also allow for the calculation of population-level  
301 parameters such as percent survivorship and the inclusion of species especially susceptible to  
302 environmental stress (because even total mortality in the neighbor removal treatment would  
303 produce a continuous variable which is necessary for the calculation of component strengths).

304

## 305 **CONCLUSION**

306 Despite the difficulties involved, studies designed to tease apart the importance of positive and  
307 negative components of interactions and their contingencies represent an exciting venue of  
308 research with the potential to greatly expand our understanding of community organization.  
309 Understanding such issues is not just an academic exercise - it is essential in order to predict how  
310 natural communities and their component parts respond to environmental heterogeneity.  
311 Furthermore, we cannot predict how the structure and organization of natural communities will  
312 respond to climate change and anthropogenic stresses until we understand how different  
313 components of the species interactions respond to such changes (Bertness et al. 1999a).

314

315

## 316 **Literature Cited**

- 317 Bertness, M. D. 1989. Intraspecific competition and facilitation in a northern acorn barnacle  
318 population.
- 319 Bertness, M. D. 1991. Interspecific interactions among high marsh perennials in a New England  
320 salt marsh.

- 321 Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh  
322 plant community.
- 323 Bertness, M. D., L. Gough, and S. W. Shumway. 1992. Salt tolerances and the distribution of  
324 fugitive salt marsh plants.
- 325 Bertness, M. D., and E. Grosholz. 1985. Population dynamics of the ribbed mussel, *Geukensia*  
326 *demissa*: The costs and benefits of an aggregated distribution. *Oecologia* 67:192–204.
- 327 Bertness, M. D., and S. D. Hacker. 1994. Physical Stress and Positive Associations Among  
328 Marsh Plants. *The American Naturalist* 144:363.
- 329 Bertness, M. D., G. H. Leonard, J. M. Levine, and J. F. Bruno. 1999a. Climate-driven  
330 interactions among rocky intertidal organisms caught between a rock and a hot place.  
331 *Oecologia* 120:446–450.
- 332 Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999b.  
333 Testing the relative contribution of positive and negative interactions in rocky intertidal  
334 communities. *Ecology* 80:2711–2726.
- 335 Bertness, M. D., and S. W. Shumway. 1993. Competition and facilitation in marsh plants.  
336 *American naturalist* 142:718–724.
- 337 Bertness, M. D., and S. M. Yeh. 1994. Cooperative and competitive interactions in the  
338 recruitment of marsh elders. *Ecology* 75:2416–2429.
- 339 Brewer, J. S., and M. D. Bertness. 1996. Disturbance and intraspecific variation in the clonal  
340 morphology of salt marsh perennials. *Oikos* 77:107–116.
- 341 Brewer, J. S., J. M. Levine, and M. D. Bertness. 1998. Interactive effects of elevation and burial  
342 with wrack on plant community structure in some Rhode Island salt marshes. *Journal of*  
343 *Ecology* 86:125–136.

- 344 Bruno, J. F., and C. W. Kennedy. 2000. Patch-size dependent habitat modification and  
345 facilitation on New England cobble beaches by *Spartina alterniflora*. *Oecologia* 122:98–  
346 108.
- 347 Callaway, R. M. 1994. Facilitative and interfering effects of *Arthrocnemum subterminale* on  
348 winter annuals. *Ecology* 75:681–686.
- 349 Callaway, R. M. 1995. Positive interactions among plants. *Botanical Review* 61:306–349.
- 350 Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of  
351 *Quercus douglasii* on understory productivity in central California.
- 352 Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to  
353 interactions in plant communities.
- 354 Claus Holzzapfel, A., and B. E. Mahall. 1999. Bidirectional facilitation and interference between  
355 shrubs and annuals in the Mojave Desert. *Ecology* 80:1747–1761.
- 356 Connell, J. H. 1961. The influence of interspecific competition and other factors on the  
357 distribution of the barnacle *Chtalamus stellatus*. *Ecology* 42:710–723.
- 358 Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal  
359 community. *Ecological Monographs* 45:137–159.
- 360 Ellison, A. M. 1987. Effects of competition, disturbance, and herbivory on *Salicornia europaea*.
- 361 Gómez-Aparico, L., R. Zamora, J. M. Gómez, J. A. Hódar, and J. Castro. 2004. Applying plant  
362 facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants.  
363 *Ecological Applications* 14:1118–1138.
- 364 Greenlee, J. T., and R. M. Callaway. 1996. Abiotic Stress and the Relative Importance of  
365 Interference and Facilitation in Montane Bunchgrass Communities in Western Montana.  
366 *The American Naturalist* 148:386.

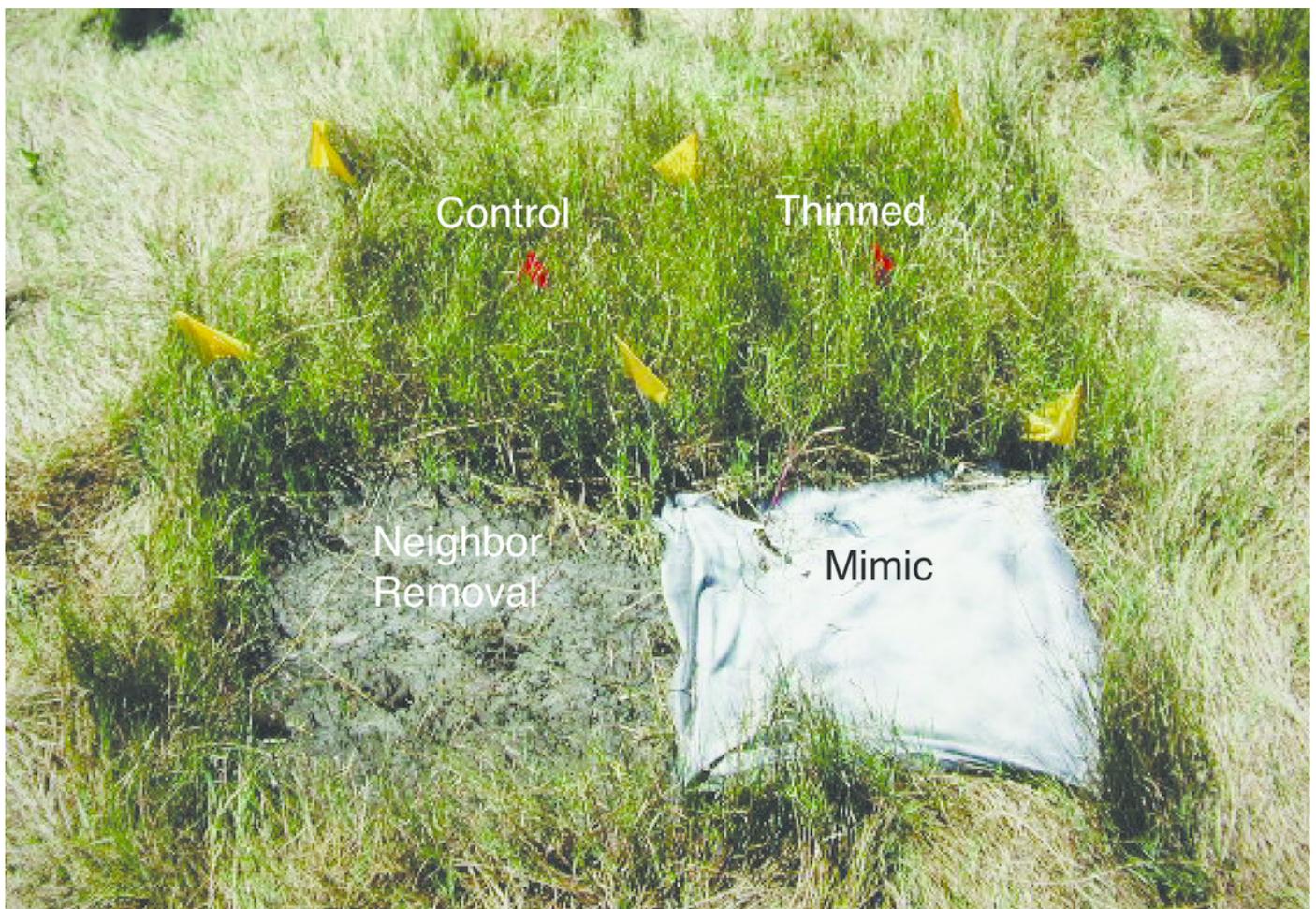
- 367 Hacker, S. D., and M. D. Bertness. 1999. Experimental evidence for factors maintaining plant  
368 species diversity in a New England salt marsh. *Ecology* 80:2064–2073.
- 369 Hacker, S. D., and S. D. Gaines. 1997. Some implications of direct positive interactions for  
370 community species diversity.
- 371 Kennedy, C. W., and J. F. Bruno. 2000. Restriction of the Upper Distribution of New England  
372 Cobble Beach Plants by Wave-Related Disturbance. *Journal of Ecology* 88:856–868.
- 373 Leger, E. A., and E. K. Espeland. 2010. The shifting balance of facilitation and competition  
374 affects the outcome of intra- and interspecific interactions over the life history of California  
375 grassland annuals. *Plant Ecology* 208:333–345.
- 376 Leonard, G. H. 1999. Positive and negative effects of intertidal algal canopies on recruitment and  
377 survival of barnacles. *Marine Ecology Progress Series* 178:241–249.
- 378 Leonard, G. H. 2000. Latitudinal variation in species interactions: A test in the New England  
379 rocky intertidal zone. *Ecology* 81:1015–1030.
- 380 Lively, C. M., and P. T. Raimondi. 1987. Desiccation, predation, and mussel-barnacle  
381 interactions in the northern Gulf of California. *Oecologia* 74:304–309.
- 382 Miller, W. B., and F. E. Egler. 1950. Vegetation of the Wequetequock-Pawcatuck tidal marshes.  
383 *Ecological Monographs* 20:143–172.
- 384 Moore, A. F. P., and J. E. Duffy. 2016. Foundation species identity and trophic complexity affect  
385 experimental seagrass communities. *Marine Ecology Progress Series* 556:105–121.
- 386 Muller, C. H. 1953. The association of desert annuals with shrubs. *American Journal of Botany*  
387 40:53.
- 388 Niering, W. A., and R. S. Warren. 1980. Vegetation Patterns and Processes in New England Salt  
389 Marshes. *BioScience* 30:301–307.

- 390 Niering, W. A., R. H. Whitaker, and C. W. Lowe. 1963. The saguaro: a population in relation to  
391 environment. *Science* 142:15–23.
- 392 Nixon, S. W. 1982. The ecology of New England high salt marshes: a community profile. U.S.  
393 Fish Wildl. Service Biol. Rep.:70.
- 394 Rand, T. a. 2000. Seed dispersal, habitat suitability and the distribution of halophytes across a  
395 salt marsh tidal gradient. *Journal of Ecology* 88:608–621.
- 396 Rand, T. a, S. M. Louda, K. M. Bradley, and K. K. Crider. 2015. Effects of invasive knapweed  
397 (*Centaurea stoebe* ssp. *micranthos*) on a threatened native thistle (*Cirsium pitcheri*) vary  
398 with environment and life stage. *Canadian Journal of Botany* 93:543–558.
- 399 Rojas-Sandoval, J., and E. Meléndez-Ackerman. 2012. Effects of an invasive grass on the  
400 demography of the Caribbean cactus *Harrisia portoricensis*: Implications for cacti  
401 conservation. *Acta Oecologica* 41:30–38.
- 402 Shumway, S. W., and M. D. Bertness. 1992. Salt stress limitation of seedling recruitment in a  
403 salt-marsh plant community. *Oecologia* 92:490–497.
- 404 Stachowicz, J. J. 2001. Mutualisms, positive interactions, and the structure of ecological  
405 communities. *BioScience* 51:235–246.
- 406 Thomson, D. 2005. Measuring the effects of invasive species on the demography of a rare  
407 endemic plant. *Biological Invasions* 7:615–624.
- 408 Yelenik, S. G., N. DiManno, and C. M. D’Antonio. 2015. Evaluating nurse plants for restoring  
409 native woody species to degraded subtropical woodlands. *Ecology Evolution*:1294.
- 410

# Figure 1

## Experimental design

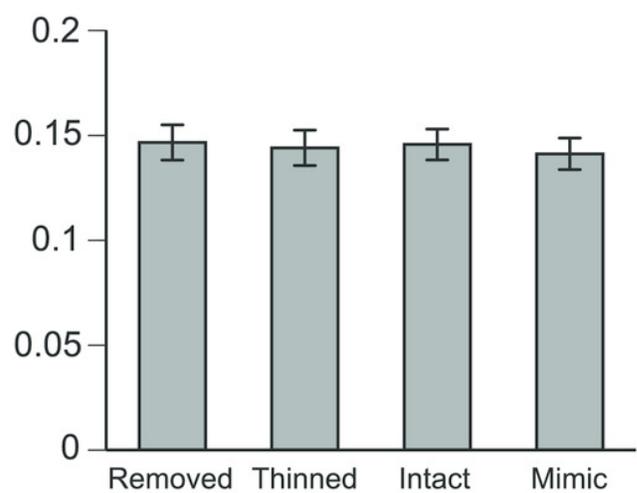
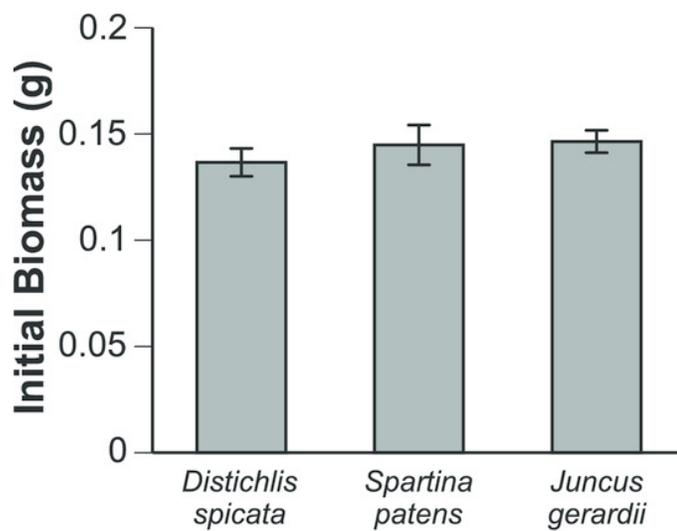
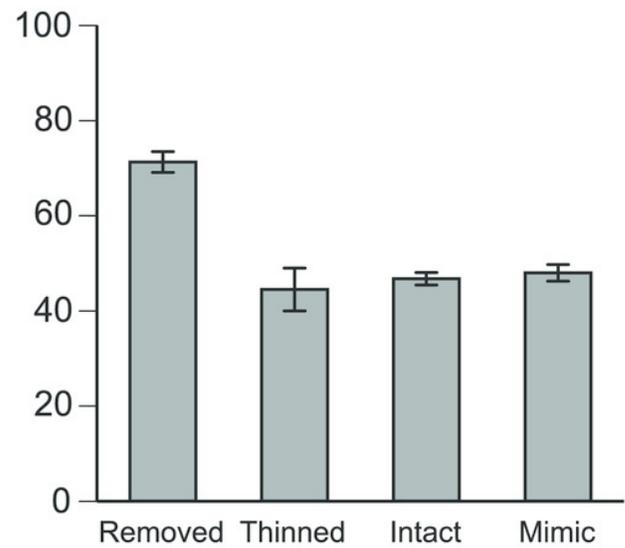
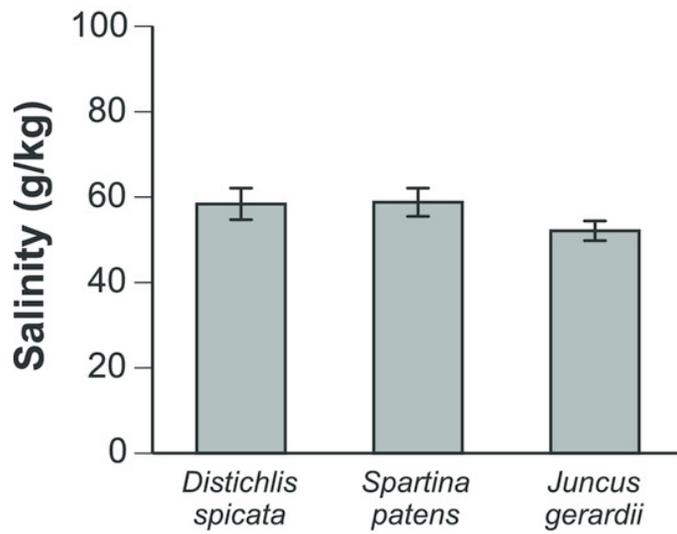
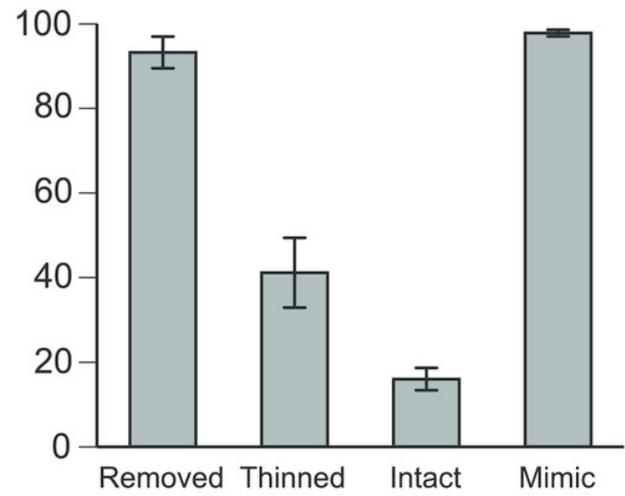
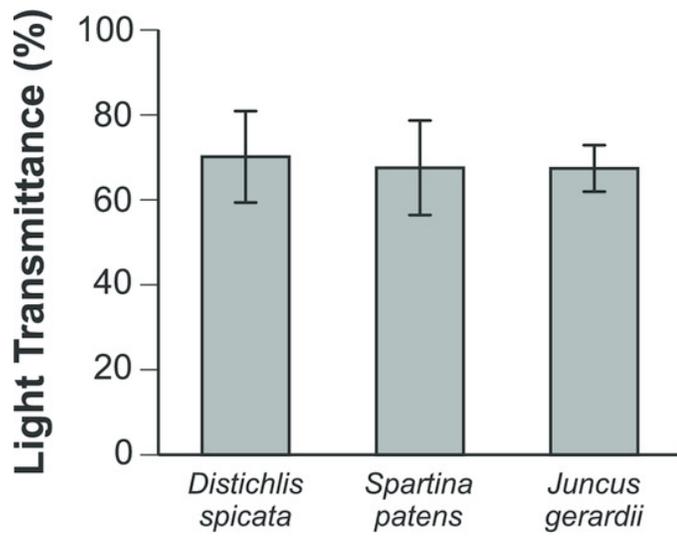
Figure 1. Photograph of a treatment block using *J. gerardi* as the transplanted matrix species with four experimental treatment plots (see labels) and a single *Aster* adult transplanted into each treatment plot. Photo credit: John Bruno.



## Figure 2

Environmental conditions and starting plant biomass.

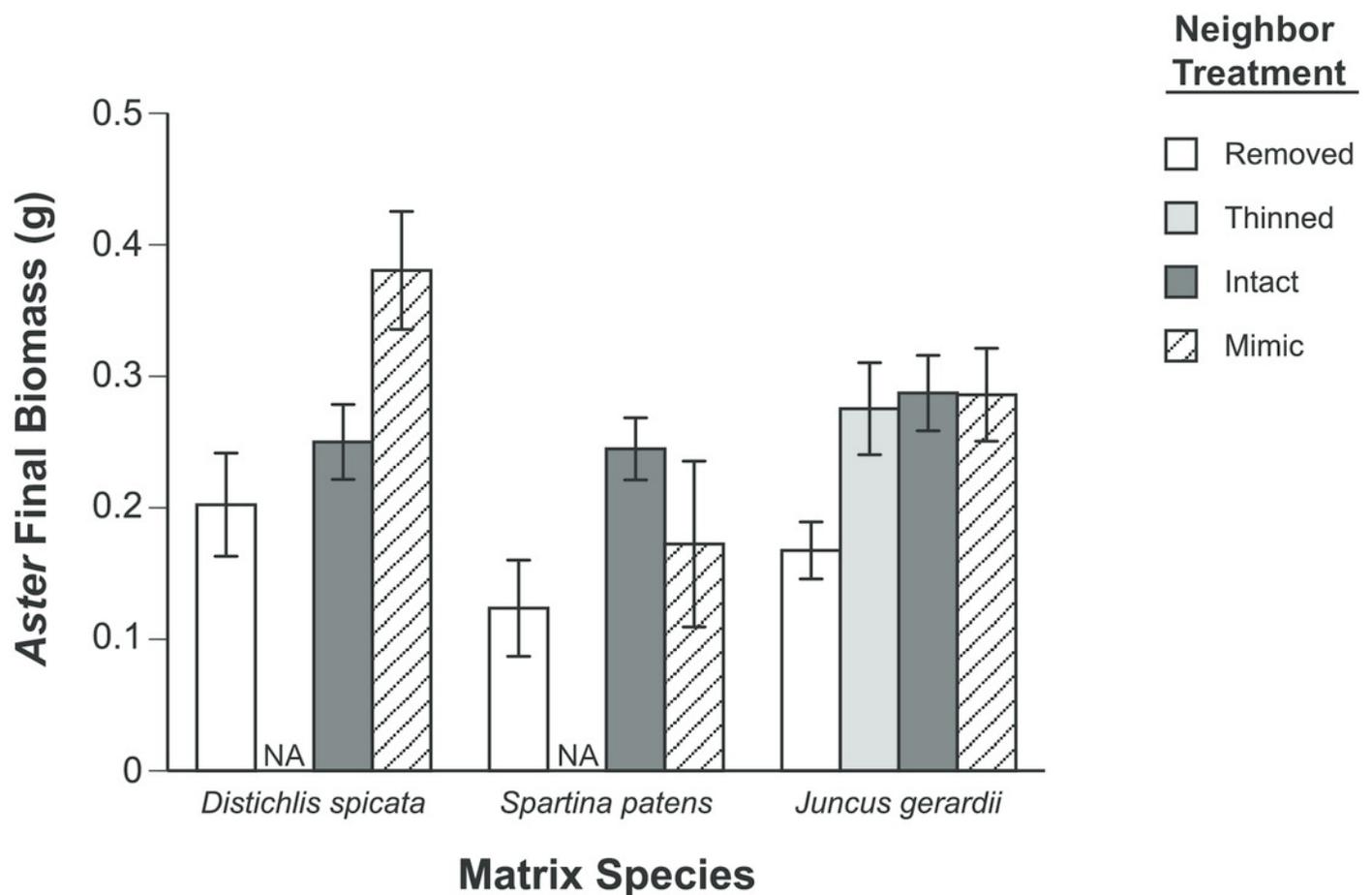
Figure 2. Effects of the matrix species (left panels) and experimental manipulations (right panels) on environmental conditions (data are means  $\pm$  1 SE from July measurements; August data are not presented but were nearly identical) and initial *Aster* biomass.



## Figure 3

Final Aster biomass.

Figure 3. Final biomass of adult *Aster* plants after 75 days in the experimental treatments and different matrix species. The thinned treatment, in which grass shoot density was reduced by 50%, was only applied in the plots with *Aster* adults transplanted into the *J. gerardi* matrix. Data are means  $\pm$  1 SE. Final *Aster* biomass varied significantly ( $P < 0.05$ ) among treatments for all three matrix species (One-factor ANOVA).



## Figure 4

### Species interaction components

Figure 4. Net, negative, and positive effects of three salt marsh matrix species on adult and juvenile *Aster* based on final biomass. Apparent differences in the strength of interaction components among the matrix species were not statistically significant ( $P > 0.05$ , ANOVA).

