

Small-mammal herbivore control of secondary succession in New England tidal marshes

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Abstract. Secondary succession is impacted by both biotic and abiotic forces, but their relative importance varies due to environmental drivers. Across estuarine salinity gradients, physical stress increases with salinity, and biotic stresses are greater at lower salinities. In southern New England tidal marshes spanning a landscape-scale salinity gradient, we experimentally examined the effects of physical stress and consumer pressure by mammalian herbivores on secondary succession in artificially created bare patches. Recovery was slower in marshes exposed to full-strength seawater, where physical stress is high. Compared to full-strength salt marshes, recovery in low-salinity marshes was much faster and was influenced by small-mammal consumers. At lower salinities, small mammals selectively ate and prevented the establishment of several native and two invasive, nuisance species (*Typha angustifolia* and *Phragmites australis*) but were unable to control the expansion of established *P. australis* stands. By controlling the establishment of competitively dominant species and the trajectory of secondary succession in low-salinity marshes, small mammals may play a cryptic keystone role in estuarine plant communities and are a critical, overlooked consideration in the conservation and management of estuarine marshes.

Key words: abiotic and biotic factors; consumer control; environmental stress models; herbivory; invasive species; New England tidal marshes; physical stress; salinity; secondary succession; small-mammal herbivores; stress gradients.

INTRODUCTION

Natural communities are mosaics of organisms in different stages of recovery from disturbances (Connell 1978, Paine and Levin 1981, Sousa 1984). Consequently, understanding secondary succession, or recovery from disturbance, has long been a central focus of studies analyzing the forces that generate the structure and organization of communities (Clements 1916, Connell and Slatyer 1977). In many cases, secondary succession is not simply recovery to a previous state, but a conditional process driven by biotic and abiotic factors that can lead to multiple persistent community states (Baldwin and Mendelsohn 1998, Bertness et al. 2002, Schmitz 2004). Understanding the relative importance of biotic and abiotic factors in shaping succession dynamics is increasingly important in human-altered landscapes, where shifts in these parameters can lead to novel climax community states.

Stress-based models (Menge and Sutherland 1987, Menge and Olson 1990) predict a general trade-off across physical stress gradients between the roles played by physical and biotic stress in secondary-succession dynamics. Harsh physical stress can limit the rate of

community recovery and minimize the importance of some biological interactions during secondary succession, such as competition and consumer pressure, while favoring other biotic interactions such as facilitative interactions driven by neighbor amelioration of physical stress (Connell and Slatyer 1977, Odum 1985, Bertness and Shumway 1993, Anderson 2007). Physically stressful conditions also favor stress-tolerant species, particularly as primary colonists (Grime 1977, Bertness et al. 1992). Under conditions of lower physical stress, the effects of competition and consumption are more important in shaping succession (e.g., Sousa 1979, Lubchenco 1983). However, the effects of herbivores have been difficult to generalize, despite long recognition of their role in succession (Connell and Slatyer 1977). Herbivory has been implicated in both accelerating (Sousa 1979, Lubchenco 1983) and slowing (Farrell 1991, Davidson 1993, Hixon and Brostoff 1996, Bertness et al. 2002, Kuijper and Bakker 2005) secondary succession, depending on the preference of herbivores for early- or late-successional species. In some cases, herbivory can push a transitioning ecosystem into an alternate state (Hixon and Brostoff 1996, Schmitz 2004). Intense herbivory during succession can select for unpalatable plants (Howe et al. 2006). By their food selection, herbivores can promote or restrict the establishment of nonnative species, favoring the establishment of unpalatable invasive plants by consuming native competitors (Ostfeld et al. 1997) or inhibiting

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invasive success by consuming exotic propagules (D'Antonio 1993, Lambrinos 2002).

Here, we present an experimental test of the way physical stress and herbivory interactively affect secondary succession in estuarine plant communities, using naturally occurring herbivore populations across a landscape-scale estuarine salinity gradient. Salinity stress plays a prominent role in shaping plant communities across estuarine gradients, affecting species pools, colonization success, and the direction and intensity of biological interactions (Odum 1988, Bertness and Shumway 1993, Crain et al. 2004, 2008, Crain 2008). In low-salinity oligohaline (0.5–5 ppt salinity) and brackish (10–20 ppt salinity) marshes, plant diversity is higher and plant competitive interactions are more intense (Crain et al. 2004). In contrast, more saline marshes (>25 ppt salinity) are less diverse because high salinity precludes survival of most wetland plants. Disturbance in salt marshes exacerbates physical stress as surficial evaporation turns soils hypersaline when the plant canopy is removed. Only a few halophytic plants can tolerate these stressful conditions. Facilitative shading by primary colonizers ameliorates hypersaline conditions and allows further recolonization (Bertness 1991, Bertness and Shumway 1993). Where salinities are lower in brackish and oligohaline marshes, salinity stress does not limit seedling recruitment (Bertness and Shumway 1993), and seed bank dynamics are an important component of successional trajectories (Leck 2003, Crain et al. 2008). In these marshes, succession follows a tolerance model, where seedlings colonize primarily but are eventually replaced by clonal vegetative growth (Baldwin and Mendelsohn 1998, Crain et al. 2008). In low-salinity marshes in North America, native clonal plants must compete for dominance of successional spaces with an aggressive monoculture-forming invasive plant, *Phragmites australis*, whose spread is facilitated by disturbance (Minchinton 2002).

Despite the key role that small mammals play in structuring many herbaceous plant communities (e.g., desert–grassland transition, Brown and Heske [1990]; tallgrass prairie, Howe et al. [2002]), rodent herbivores traditionally have been considered to play a minor role in structuring North American estuarine marsh plant communities. In European salt marshes, herbivory plays an important role in primary succession across landscapes; grazing by hares can delay establishment of late-successional species by >25 years (van der Wal et al. 2000). In New England, herbivory by small mammals occurs in all salt marsh plant zones (Howell 1984), and consumer pressure is relatively constant at marshes of different salinity across estuaries (Crain 2008). New evidence shows that small mammals can significantly influence plant species interactions in tidal marshes, particularly in lower salinity marshes (Crain 2008). Top-down control by small mammals may be even more important during secondary succession, when colonizing seedlings and runners appeal to small-mammal herbi-

vores that prefer undefended, protein-rich plants (Bucyanayandi and Bergeron 1990, Tahvanainen et al. 1991).

To examine the relative importance of herbivory and environmental stress during secondary succession of coastal marsh vegetation, we studied the speed and community composition of plant recovery in artificial bare patches where small-mammal herbivore pressure was experimentally manipulated in estuarine marshes of differing salinities. Previous research in this system has shown that secondary succession proceeds much more quickly in low-salinity marshes due to opportunistic colonization by a substantial and diverse seed bank (Crain et al. 2008), and that the importance of top-down control of plant species interactions by small mammals increases in lower salinity marshes compared to salt marshes (Crain 2008). We hypothesized that the relative importance of small-mammal consumers in driving the pace and species composition of secondary succession will be greater in low-salinity marshes. Additionally, we questioned if the role of herbivores during secondary succession differs fundamentally from their role in undisturbed environments by conducting a simultaneous study of undisturbed, mature plant communities where we experimentally manipulated small-mammal herbivore pressure.

METHODS

Study sites

Our work was conducted in estuarine marshes in Narragansett Bay, Rhode Island, USA. Previous work has shown that the sites used are representative of marshes throughout Narragansett Bay (Crain et al. 2004). Salt marsh sites ($n = 8$) were identified in the Nag Creek system on Prudence Island, part of the Narragansett Bay National Estuarine Research Reserve. Brackish ($n = 8$) and oligohaline marsh sites ($n = 8$) were located along the Barrington River. Additional work on *Phragmites australis* was done in an oligohaline marsh system along the Palmer River ($n = 10$ sites). Marshes in this region experience diurnal tides, with a maximum tidal range of 2 m.

Nag Creek salt marshes exhibit typical zonation of dominant plant species, with a low marsh of *Spartina alterniflora*, *Spartina patens* dominating intermediate elevations and outcompeted at high elevations by *Juncus gerardii*, and an upland fringe of *Iva frutescens* and *P. australis* (Bertness and Ellison 1987). The few other plant species common to these zones include *Distichlis spicata*, *Limonium nashii*, and *Salicornia europaea*. The brackish marsh plant assemblage is similar to the salt marsh, but with the additional dominant *Scirpus robustus*, and more species interspersed within the monocultures, such as *Solidago sempervirens* and *Atriplex patula*. Dominant plant species at the oligohaline sites also include *Typha angustifolia*, and a still greater diversity of species growing within the *J. gerardii* and *S. patens* zones (e.g., *Pluchea purpureascens*, *Agrostis*

stolonifera, and *Carex hormathodes*) (see Crain et al. [2004] for site characterizations and species assemblages). This experiment was conducted at intermediate elevations at all sites, where *S. patens* was the dominant plant species across the entire gradient. Mammal trapping in the fall of 2004 found two species of small rodents, the meadow vole (*Microtus pennsylvanicus*) and the white-footed mouse (*Peromyscus leucopus*) commonly present at all salinities (Crain 2008).

Survey of natural disturbance-generated bare space

To examine the natural abundance and distribution of disturbance-generated bare space across the estuarine gradient, we conducted a field survey in May 2007. The primary source of disturbance in New England tidal marshes is smothering by wrack mats, aggregations of dead plant stems that form in the high marsh in the spring (Bertness and Ellison 1987). We quantified bare space along 25×1 m transects in salt, brackish, and oligohaline marshes ($n = 20$ sites per salinity category). Transects were initiated at the high marsh edge and ran perpendicular to the shoreline to include all vegetation zones. When bare patches were encountered, we measured their area within the transect (length \times width approximation). Bare patches smaller than 0.1 m^2 were not included, as these areas are entirely shaded by neighboring vegetation and do not follow the same successional dynamics. Because recovery time varies across estuarine salinity gradients (Crain et al. 2008), we varied our classification of bare area in marshes of different salinity to standardize as best as possible for bare areas established within the season. In oligohaline and brackish marshes, seedling-only dominated areas were included in the survey because they probably represented bare area generated within the year. In contrast, large hypersaline bare areas in salt marshes were excluded because they can persist for numerous seasons after a disturbance event. Instead, only areas with evidence of recently killed vegetation (i.e., wrack still present or decomposing biomass) were included.

Do consumers or physical stress affect secondary succession trajectories?

To test the relative importance of consumers and physical stress on secondary succession dynamics of tidal marsh vegetation, we performed a patch recovery experiment in communities that varied in salinity stress and mammalian consumer pressure. Three replicate bare patches were established in eight marsh sites of each salinity level (salt, brackish, and oligohaline) and were randomly assigned a caging treatment (cage, cage control, control) for a total of 72 disturbance plots. Bare patches were created in the fall of 2004 with foliar application of Roundup, a general, systemic herbicide (Montsanto, Marysville, Ohio, USA) to 0.5×0.5 m plots marked with PVC corner flags. Dead plant material was removed with a weed-whacker in the following spring. The resulting bare patches, devoid of

living stems and roots, closely mimicked natural wrack disturbances (Bertness 1991).

Herbivore exclusion cages were installed in May 2005. Cages ($1 \times 1 \times 1$ m) were constructed of galvanized hardware cloth (1-cm mesh) stapled to wooden corner stakes. The mesh size was chosen to be small enough to exclude even juvenile rodents, but large enough to allow passage of smaller herbivores and detritivores, such as insects, snails, and crustaceans. Smaller mesh sizes are probably necessary to exclude these macroinvertebrates (2-mm mesh, Bell [1980]; organdy gauze, Denno et al. [2000]). The bottom edges of the cages were inserted 5 cm into the peat to prevent ground access by rodents. The tops of cages were left open to permit access by flying insects and birds. We frequently observed insects (including lepidopteran, homopteran, coleopteran, and orthopteran species) within the cages. Large ground-dwelling insects potentially could have been excluded from these plots, but the primary caging effect was small-mammal exclusion. Observationally, there were no differences in the degree of insect damage to marsh plants (i.e., gnashed or shredded leaves, necrotic spots indicative of planthopper damage; Bertness et al. 2007) across caging treatments. Cage controls ($1 \times 1 \times 0.5$ m tall) used a similar design, but were raised 0.25 m above the surface to allow ground access while controlling for experimental artifacts of cages, such as shading. We frequently observed plant clippings and rodent feces in cage control and control plots, consistent with visitation by small-rodent herbivores. This evidence was never observed in rodent enclosure plots, confirming that the cages effectively controlled rodent access.

Species cover was quantified every two weeks for the first six weeks of the experiment, after which recovery was assessed at the end and beginning of the growing season for three years (2005–2007). Cover was measured using the point-intercept method: the plot was overlaid with a 10×10 string grid (0.5×0.5 m area), and species identity (or bare space) was noted under each string intersection (100 points) to determine the percent cover of each species. The same person (K. Bromberg Gedan) took species cover data on all occasions.

Does herbivory control the expansion of an established invasive plant?

In order to test whether rodent herbivory effects were similar in invading plant stands and in recovering plots, we manipulated consumer pressure on the expanding boundary of mature stands of *Phragmites australis*, a rapidly spreading invasive species in New England estuarine marshes. We studied *P. australis* in oligohaline locations because the plant grows most aggressively at low salinities (Chambers et al. 1999).

We randomly located 30 0.5×0.5 m plots along 200 m of shoreline, with individual plots separated by at least 10 m. We established plots along the boundary of a dense *P. australis* stand, where *P. australis* was expanding into a mix of *S. patens* and *J. gerardii*. Each

plot was randomly assigned an herbivory treatment (cage, cage control, control). Cages ($0.5 \times 0.5 \times 1$ m tall) were made of black plastic Vexar (5-mm mesh). Flexible Vexar mesh was used to avoid damaging brittle *P. australis* stems, which extended several meters above the top lip of the cage. Although the smaller mesh size may have excluded a smaller class of ground-dwelling insects, cages were again open on top and allowed access by flying insects and birds. Cage controls had two 0.3×0.1 m (width \times height) entranceways cut in the bottom and oriented parallel to the stand border. We installed cages and marked plots with PVC corner flags in September 2004. Initial *P. australis* stem density in all plots was 38.6 ± 2.6 stems/m² (mean \pm SE), with no significant difference between treatments. Within each plot, stems of *P. australis* were counted at the beginning and end of each growing season, 2004–2007. Although trapping was not repeated at the Palmer River location, visual observations of meadow voles were made on several occasions and clipped plants and feces found in controls and cage controls supported the conclusion that herbivore identity along the Palmer River is comparable to sites along the Barrington River.

Data analysis

We tested for differences in wrack-generated bare space across the salinity gradient with a one-way ANOVA on total bare area per transect, with salinity level as the independent variable. The secondary succession experiment cover data, collected as percentages, was arcsine square-root transformed to avoid restrictions on bounded data and was analyzed in three ways. (1) Speed of recovery was analyzed with a repeated-measures ANOVA (rm-ANOVA) of a split-plot design (Quinn and Keough 2002), testing the effects of sampling dates (time period), salinity (between-plot factor), block nested within salinity, and caging (within-plot factor) on bare space cover (response variable). (2) Species-specific effects of treatments were determined by a split-plot ANOVA, with final cover data of all species (and bare space) as the response variables, and the same treatment effects as in (1). (3) Community-level differences in diversity and species composition of recovered bare patches were analyzed using species richness, Shannon diversity index (Margalef 1958), and principal components analysis (PCA). Species richness data and Shannon diversity index values were analyzed with a split-plot ANOVA as previously described. We used PCA to determine if experimental treatments explained variation between communities. To deconstruct the multivariate PCA, we used an eigenvector cutoff of ± 0.3 to identify the plant species most influential in explaining community variance. Finally, the effect of herbivory on established *P. australis* expansion was tested using an rm-ANOVA of stem density, with caging as the treatment effect and sampling date as the time period. PCA was done with PC-ORD software (Version 5, MjM Software 1999). All other analyses were done

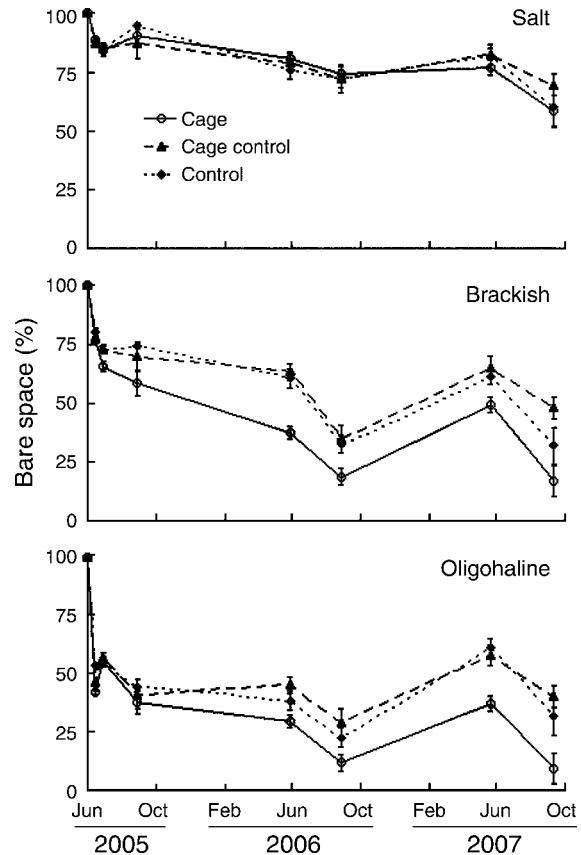


FIG. 1. Experimental bare space over time (mean \pm SE; $n = 8$ Rhode Island marsh sites) in herbivory manipulation plots across the salinity gradient. Data were taken three times over the first six weeks of the experiment and then at the beginning (June) and end (September) of the growing seasons of 2005, 2006, and 2007. Cage treatments excluded small mammalian herbivores. Both cage control and control treatments allowed herbivore access.

with JMP statistical software (Version 5.0.1.2, SAS Institute 2003).

RESULTS

Distribution of disturbance-generated bare space

Wrack-generated bare space was clearly visible at all marshes, but the amount of bare space varied with salinity (one-way ANOVA, $F_{2,51} = 5.909$, $P < 0.01$). Oligohaline marshes had the least disturbance space, with $<1\%$ unvegetated. Wrack-generated bare space was much more common in higher salinity marshes. Brackish and salt marshes had nearly an order of magnitude more disturbance-generated bare space (8% and 5%, respectively) than oligohaline marshes.

Do consumers or physical stress affect secondary succession trajectories?

The interaction of salinity and herbivory affected the speed of secondary succession (rm-ANOVA $F_{4,42} = 2.68$, Wilks' lambda < 0.05). Recovery, operationally defined

TABLE 1. Summary (F values) of the secondary succession experiment split-plot ANOVA on percent cover of all species present in Narragansett Bay study marshes (Rhode Island, USA) on the final sampling date in September 2007.

Species	Salinity	S; df = 2, 29	B(S); df = 21, 29	H; df = 2, 29	S × H; df = 4, 29
<i>Atriplex patula</i>	b, o	4.25*	1.11	0.74	0.79
<i>Limonium nashii</i>	s	4.04*	0.65	1.83	1.83
<i>Juncus gerardii</i>	b, o	3.52*	0.69	0.86	0.51
<i>Spartina alterniflora</i>	s	4.84*	1.31	1.24	1.24
<i>Iva frutescens</i>	b	5.69**	1.42	0.01	0.01
<i>Salicornia europaea</i>	s	7.25**	3.79***	0.31	1.32
<i>Distichlis spicata</i>	s, b, o	3.37*	2.34**	0.23	0.54
<i>Carex hormathodes</i>	o	23.43****	3.36***	0.77	0.79
<i>Agrostis stolonifera</i>	o	33.59****	12.22****	1.56	1.56
<i>Pluchea purpurescens</i>	o	6.74**	2.77**	2.35	2.35
<i>Spartina patens</i>	s, b, o	16.83****	2.20*	5.11*	0.56
Bare space	s, b, o	90.19****	4.01****	40.34****	4.3**
<i>Solidago sempervirens</i>	b, o	85.43****	6.36****	7.28**	4.16**
<i>Phragmites australis</i>	b, o	5.54**	1.18	9.37***	2.61*
<i>Typha angustifolia</i>	o	5.09*	0.98	5.09*	5.12**
<i>Scirpus robustus</i>	b, o	2.23	1.00	6.69**	2.22
<i>Panicum virgatum</i>	o	1.80	0.78	0.45	0.45

Notes: Factor abbreviations: S, salinity; B(S), block nested within salinity; H, herbivory; S × H = salinity × herbivory interaction. Salinity levels at which the species was present in experimental plots are: s, salt; b, brackish; o, oligohaline.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

as the amount of bare space remaining in plots, was affected by herbivory in brackish and oligohaline marshes, but not in salt marshes (Fig. 1). Herbivory slowed recovery by maintaining bare space. In brackish marshes, control plots contained twice as much bare space as caged plots after three years (32% vs. 17%), and in oligohaline marshes, control plots were three times as bare (31% vs. 9%). Salinity stress also slowed secondary succession. Salt marsh control plots were still >50% bare after three years ($60\% \pm 8.0\%$, mean \pm SE; Fig. 1), but brackish and oligohaline control plots recovered twice as fast, with only $32\% \pm 4.4\%$ and $31\% \pm 4.1\%$ bare after three years, respectively. All of these differences became apparent in the first year of recovery (Fig. 1).

Salinity and herbivory each had large effects on species composition of recovered communities (Table 1, Appendix A). Only two species, *S. patens* and *D. spicata*, were present over all salinity levels. The other 14 species were unique to either salt marshes or brackish and oligohaline locations. Although not statistically significant in the split-plot ANOVA model, species richness and diversity tended to increase as salinity decreased (Table 2), consistent with previous work (Odum 1988, Crain et al. 2004). The main effect of herbivory was to

reduce species diversity, with higher Shannon index and richness values of species diversity in caged treatments (Table 2; for Shannon, $F_{2,42} = 3.21$, $P < 0.05$; for richness, $F_{2,42} = 8.76$, $P < 0.001$).

Species varied greatly in their responses to physical and consumer stresses. These responses can be grouped into three general types: (1) The salinity treatment significantly affected species cover, whereas the herbivory treatment did not. This applied for all of the species at salt marsh sites, except *S. patens*, and the majority of species in brackish and oligohaline sites. In many cases, salinity effects were accompanied by a significant block effect (Table 1), indicating small-scale spatial variation in species distributions between sites. (2) Salinity and herbivory treatments interactively affected species cover. In these cases (bare space, *S. sempervirens*, *P. australis*, and *T. angustifolia*; Table 1, Figs. 2 and 3), significant herbivory effects occurred in the brackish and/or oligohaline sites, but the species was absent from salt marsh sites, leaving no possibility for herbivory effects there (except for bare space, which was overrepresented at salt sites). (3) There was a significant effect of only herbivory for one species, *Scirpus robustus*, which, while also absent from salt marsh sites, was in low abundance

TABLE 2. Species richness and Shannon diversity index (mean \pm SE) within experimental secondary succession communities in September 2007, three years after the removal of vegetation.

Measurement	Salt			Brackish		
	Cage	Cage control	Control	Cage	Cage control	Control
Species richness	2.63 \pm 0.26	2.25 \pm 0.25	1.63 \pm 0.26	4.00 \pm 0.57	2.13 \pm 0.30	2.50 \pm 0.27
Shannon diversity	0.83 \pm 0.08	0.74 \pm 0.08	0.70 \pm 0.07	1.04 \pm 0.12	0.88 \pm 0.07	0.82 \pm 0.07

Notes: Herbivory manipulations consisted of 1-m² cage, cage control, and control treatments. Cages of wire mesh excluded small mammal herbivores. Cage controls mimicked the structural effects of cages but allowed herbivore access at the ground. Controls had no caging structure and were also exposed to herbivores.

(<2%) at all sites, diminishing the ability for detection of an interactive effect. *S. patens* did not fit into this scheme; it experienced independent significant effects of herbivory and salinity treatments, indicating that herbivory effects on *S. patens* did not vary over the salinity gradient. *S. patens* was less abundant in cage controls than in control and caged treatments, and *S. patens* was more abundant at brackish than salt sites and least abundant at oligohaline sites (Fig. 3). In all other cases, control and cage control treatments did not differ.

We used principal components analysis to examine how overall species composition of experimental communities varied with salinity and herbivory treatments. PCA of community composition at the end of three recovery seasons showed differences between communities explicable by both salinity and herbivory treatment effects, as seen by the partitioning of communities by salinity levels and herbivore treatments, mainly along the first axis (Fig. 4). The two primary axes explained 29% of the variance in species composition among all experimental replicates. The spread of PCA scores among herbivore treatments is greatest in the oligohaline communities, intermediate in the brackish, and the salt communities are most tightly clustered (Fig. 4), indicating a diminishing role of herbivores in driving community composition in succession plots from low-salinity to high-salinity marshes.

There were no natural breaks in the PCA eigenvector values that indicated the influence of each species in each principal component. However, an eigenvector cutoff of ± 0.3 indicated the eight most important space-holders in shaping community differences: *C. hormathodes*, *A. patula*, *S. sempervirens*, *S. robustus*, *P. australis*, *T. angustifolia*, *S. patens*, and bare space (Appendix B). Of these eight, the first six were found solely in lower salinity marshes, whereas *S. patens* and bare space were more abundant at higher salinities (Fig. 3). Of the lower salinity species, all except *C. hormathodes* showed higher abundance in exclusion cages (Fig. 3). *S. robustus*, *T. angustifolia*, and *P. australis* were rare to absent in communities with herbivore access (Fig. 3).

*Does herbivory control the expansion
of an established invasive plant?*

Rodent herbivores did not control the growth of *P. australis* within established stands. An rm-ANOVA testing the effects of sampling time and herbivore



FIG. 2. Photographs of plant communities in experimental bare patches after three years of recovery. Bare patches in all salinities were placed in a background dominated by *Spartina patens*. (A) Oligohaline enclosure with abundant *Typha angustifolia* and *Carex hormathodes*. (B) Brackish enclosure colonized by *Phragmites australis* and *Solidago sempervirens*. (C) Salt enclosure, still with patches of bare space, but being recolonized by *Spartina patens*. Enclosures are all 1 m on a side. Photo credits: K. B. Gedan.

TABLE 2. Extended.

Cage	Oligohaline	
	Cage control	Control
5.38 \pm 0.56	4.63 \pm 0.32	4.63 \pm 0.53
1.27 \pm 0.12	1.15 \pm 0.05	1.26 \pm 0.08

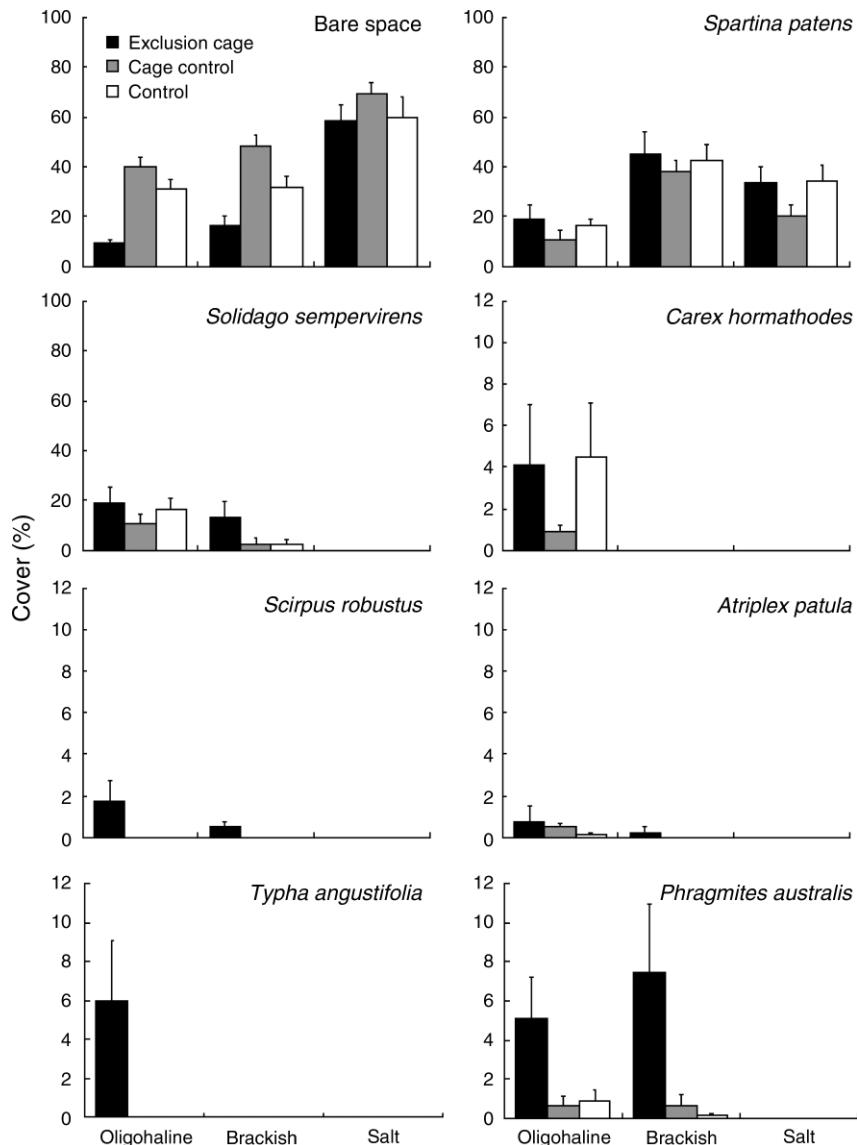


FIG. 3. Species cover (mean + SE) for the eight plant species that explained the most variance between final species cover of experimental secondary succession plots ($n = 8$ marsh sites per herbivory treatment per salinity level). Note that the y -axes differ in scale: abundant species are shown on a 0–100% scale, whereas less abundant species are shown on a 0–12% scale.

treatment showed no significant effect of herbivore treatment. Although there was a significant effect of herbivores in both 2006 sampling periods when analyzed independently (one-way ANOVA of stem density: beginning of 2006, $F_{2,26} = 7.60$, $P < 0.01$; end of 2006, $F_{2,26} = 4.39$, $P < 0.05$), this did not result in a significant herbivory effect or an herbivory \times time interaction in the rm-ANOVA. There was a significant effect of time ($F_{6,21} = 8.65$, Wilks' lambda < 0.0001), due to an increase in the density of *P. australis* stems in experimental plots as the invasion progressed, from 38.6 ± 2.6 stems/m² (grand mean \pm SE) in fall 2004 to 60.2 ± 3.7 stems/m² in Fall 2007 (Fig. 5).

DISCUSSION

Our results reveal that the trajectory of secondary succession of New England estuarine plant communities varied across landscape-level spatial scales, following basic predictions of environmental stress models. In physically stressful salt marsh habitats, secondary succession was slow and mediated largely by physical processes, whereas in less stressful brackish and oligohaline marshes, herbivory by small-mammal grazers slowed the rate of succession and radically altered plant community structure. Thus, although the importance of small-mammal herbivores has been unrecognized in the dynamics of estuarine marsh plant communities in New

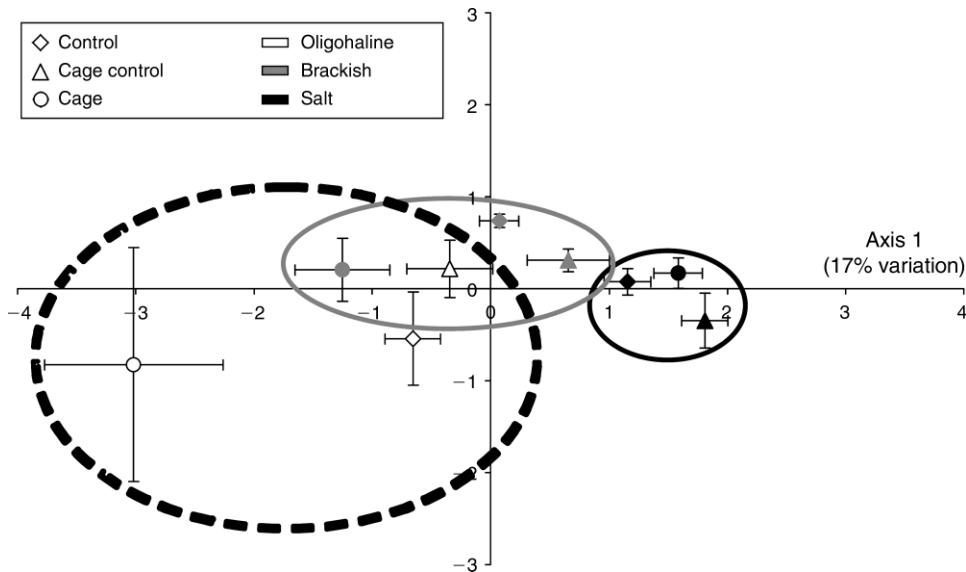


FIG. 4. Principal components analysis (PCA) of plant community composition on the final sampling date (in September 2007). Each point represents the mean \pm SE of eight replicate community PCA scores. Diamonds represent control treatments, triangles are cage control, and circles are cage treatments. The fill of each symbol indicates the salinity level (open, oligohaline; gray, brackish; black, salt). Ovals are drawn around each salinity level (black dashed line around oligohaline points). Variables responsible for score differences are discussed in *Results: Do consumers or physical stress affect secondary succession trajectories?*

England, our results suggest that they may control the invasability of brackish and oligohaline marshes and play a keystone role in these threatened communities by controlling the establishment of competitively dominant invasive plants.

Marsh dynamics, secondary succession theory, and stress models

Drivers of secondary succession in New England coastal marshes shift markedly across landscape-level salinity gradients. In salt marshes, succession proceeds via facilitation; recovery of the clonal dominant *S. patens* is dependent on amelioration of high salinities by halophytic primary colonizers that shade the substrate (Bertness and Ellison 1987, Bertness and Shumway 1993, Brewer et al. 1998). In contrast, in less physically stressful oligohaline and brackish marshes, succession proceeds via a tolerance model, as rapid colonization by opportunistic forbs blocks other species and competitively slows the ultimate recovery of dominant graminoids (Crain et al. 2008). Consistent with earlier results, we found that the climax species *S. patens* recovered fastest in brackish marsh (Fig. 3), where it is not slowed by physical stress, as in salt marsh, or impeded by competition with forb species, as in oligohaline marsh.

Here, we have found that consumer effects are another key component of successional trajectories in low-salinity marshes, affecting both speed of recovery and community composition. Consumer pressure in lower stress oligohaline and brackish marshes resulted in *S. patens*-dominated communities, superficially similar to those in the salt marsh, via a different successional

pathway, in which herbivores selectively limited the establishment of many plant species until herbivore-resistant species and superior competitors filled in disturbed areas.

In comparison to salt marshes, plant secondary succession in oligohaline and brackish marshes progressed much faster and involved more species. In the absence of physical stress limitation, herbivory by small mammals was important in oligohaline and brackish marshes in controlling speed and community composition during secondary succession. Thus, our results support the predictions of conceptual environmental stress models, largely based on the importance of

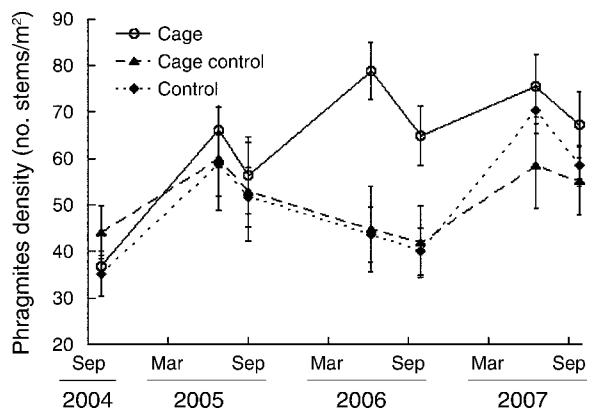


FIG. 5. Density (mean \pm SE, $n = 10$ replicates) of *Phragmites australis* stems over time in herbivore manipulation plots in an established *P. australis* stand in an oligohaline marsh.

physical stress and consumer pressure being inversely related in driving process and pattern in natural communities (Menge and Sutherland 1987, Bruno et al. 2003).

We found natural disturbance spaces to be more common in higher salinity marshes. Although this was only one year of data, it suggests that the extent of disturbance, in addition to the mode of recovery, may vary over estuarine gradients. The relatively greater abundance of disturbed areas in higher salinity marshes indicates that plant species turnover during succession will be greatest in brackish communities, where disturbance occurs more extensively than in oligohaline marsh and where plant regrowth, not limited by physical stress, occurs more quickly and with greater species diversity than in salt marsh.

The role of herbivory in marsh succession and community structure

Our results bolster the growing realization that herbivory is a far more important driving force in marsh plant communities than has been assumed (Teal 1962). Numerous studies have supported the general hypothesis that, although salt marsh primary production historically was largely controlled by bottom-up physical forces, human disturbance is triggering consumer control of primary production in marshes (Bertness and Silliman 2008). Cases ranging from herbivory by agriculturally supplemented goose populations (Jeferies et al. 2006) and snail herbivores released from crab predation (Silliman and Bertness 2002) to rampant herbivory by introduced nutria (Geho et al. 2007) and nutrient-stimulated insect consumers (Bertness et al. 2007), point to human impacts of overharvesting, species introductions, and eutrophication triggering herbivore control. However, in contrast to these instances of human stimulation of top-down control of marsh plant communities, small mammals in low-salinity marshes seem to be an example of consumer control of marsh plant community structure without any known human trigger.

In low-salinity marshes, small-mammal herbivores slowed succession by maintaining bare space (Fig. 1) and, more significantly, determined community composition of successional spaces by deflecting recovering plant communities from an alternate stable state dominated by invasive clonal plants. This alternate state was realized in herbivore exclosures in oligohaline and brackish marshes, where *T. angustifolia* and *P. australis*, two common and aggressive invasive plants in tidal marshes, dominated experimental communities (Fig. 2). Temporal and spatial variation in the intensity of small-mammal herbivory may allow establishment of non-*Spartina* patch dominants in periods or areas of low herbivore intensity and may contribute to the absence of clear zonation among dominant plants in lower salinity wetlands (Odum 1988).

Implications for wetland management and conservation

Our results suggest that in New England oligohaline and brackish estuarine marsh plant communities, previously overlooked small-mammal herbivory is critical in maintaining native plant diversity and community structure. Many of the plants preferred by rodents in brackish and oligohaline marshes are aggressive, clonal species that form dense monocultures if allowed to become established. These species include the sedge *S. robustus*, a native mesohaline dominant, and *T. angustifolia* and *P. australis*, two hybrid invaders and nuisance species in many North American wetland systems (Saltonstall 2002, Selbo and Snow 2004).

Although diversity increased in rodent exclusion cages over the course of this study, over longer timescales these aggressive clonal plants probably would have outcompeted most native plants (Minchinton et al. 2006). The invasion of North American wetlands by clonal plants is displacing native plants and animals and altering plant structure and wetland geomorphology (Chambers et al. 1999, Zedler and Kercher 2004). Disturbance fosters establishment of both *T. angustifolia* and *P. australis* (Galatowitsch et al. 2000, Minchinton and Bertness 2003), but, as our results reveal, small-mammal populations cryptically control the establishment of these plants following disturbance. Our results also indicate that once these clonal invasive species have become established, at least in the case of *P. australis*, small-mammal herbivory can no longer contain their spread. The successful establishment of these plants in oligohaline and brackish marshes is dependent on spatial or temporal refuge from rodent herbivores.

Clearly, invasive plant species have thrived in tidal wetlands despite the ability of rodent herbivores, as shown by our research, to limit their establishment. Rodents are a single filter for invasions and other factors contribute to invasive performance. Invasive success in wetlands has also been linked to high nutrient availability, for example, and the clonal growth strategy (Amsberry et al. 2000, Zedler and Kercher 2004). However, the persistence of invasive species does not discount the role of mammalian herbivores in controlling their establishment. Our research shows that, following disturbance, rodents are remarkably effective in preventing the success of invasive propagules in low-salinity marshes, where elsewhere *T. angustifolia* and *P. australis* prosper. Given this important role, healthy rodent communities can limit the need for expensive and potentially hazardous invasive control techniques. Scientists and managers need more information on rodent population dynamics and resource use in tidal marshes to know when and where rodent herbivory will limit invasive plant establishment.

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APPENDIX A

Species cover within experimental secondary succession communities in September 2007, after three recovery growing seasons (*Ecological Archives* E090-030-A1).

APPENDIX B

PCA eigenvectors from the first and second primary axes for all species (*Ecological Archives* E090-030-A2).