

Patch size-dependent community recovery after massive disturbance

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Abstract. Massive anthropogenic and climate-related disturbances are now common in ecosystems worldwide, generating widespread die-off and subsequent community recovery dominated by remnant-patch dynamics rather than open-gap dynamics. Whether communities can recover and, if so, which factors mediate recolonization rate and extent remain unresolved. Here we evaluate recolonization dynamics of southern U.S. salt marshes that experienced extensive, drought-induced die-off of the foundation species *Spartina alterniflora* over the previous decade. Surveys of Georgia (USA) salt marshes showed little seedling recruitment in die-off areas but persistence of *Spartina* particularly in large, rather than small, remnant patches. Given this natural variation in remnant patch size, we conducted field experiments to test whether key plant-controlling biotic (grazing, plant neighbor presence) and abiotic (water availability) factors differentially impact *Spartina* recolonization at small and large-patch scales. In the small-patch (<1 m²) experiment in 2009, removing grazers and plant neighbors prompted dramatically higher expansion and growth of *Spartina* relative to controls, while adding freshwater to reduce water limitation had little effect. In contrast, large-patch (>20 m²) borders advanced significantly over the same time period regardless of grazer or neighbor removal. We continued the large-patch experiments in 2010, a year that experienced drought, and also added freshwater or salt to borders to modify ambient drought stress; overall, borders advanced less than the previous year but significantly more where neighbors were removed or freshwater added. Thus, water availability appears to mediate *Spartina* recovery by fueling large-patch expansion during wet summers and intensifying interspecific competition during drought. Combined, these findings suggest ecosystems can recover from massive disturbance if remnant foundation species' patches are large enough to overcome biotic inhibition and successfully expand during periods of relaxed abiotic stress.

Key words: climate change; competition; drought; foundation species; herbivory; mudflats; patch dynamics; resilience; salt marshes, Georgia, USA; size-dependent recolonization processes; *Spartina alterniflora*; succession.

INTRODUCTION

Disturbance has been recognized as a central driver of community organization and ecosystem functioning since the publication of Dayton's work on disturbance dynamics on rocky shores nearly 40 years ago (Dayton 1971). Coincident with this work, key theories about disturbance effects on community structure and stability emerged, including the intermediate-disturbance (Grime 1973, Connell 1978), forest-gap (Ricklefs 1977) and alternate-stable-state (Lewontin 1969) hypotheses that have provided a foundation for decades of ecological debate and experimental scrutiny. Over recent years, climate change and human activities have amplified the magnitude of disturbance events (Folke et al. 2004, Lamb et al. 2005), challenging ecologists to evaluate the applicability of existing disturbance models to systems where extensive swaths of the biotic community have been wiped out (e.g., mass coral bleaching, rainforest deforestation). To understand the implications of these

heightened disturbance conditions for community structure and stability, a new conceptualization of "patch" dynamics seems necessary. Historically, studies of disturbance have focused on processes mediating closure of discrete, open patches embedded within spatially dominant biotic community matrices, i.e., open-gap dynamics and modeling (Fig. 1a; e.g., Asner et al. 2004). To best replicate dominant natural patterns, ecologists should now shift their focus toward identifying processes that enhance or impede expansion of remnant patches lingering within largely open, disturbed habitats (Fig. 1b) and utilize this information in conservation to augment the rate and extent of community recovery.

Extensive research on open-patch dynamics has demonstrated the importance of physical attributes of patches, such as their size and spatial distribution, in mediating the rate and pattern of community recolonization (Connell 1978). Of these, patch size has emerged as a key deterministic factor in recolonization trajectories because the importance of physical stress (i.e., light, space, nutrient availability, wind or wave exposure) and species interactions (i.e., competition, facilitation, top-down control) in mediating the rate of patch closure often shifts as the sizes of disturbed patches increase

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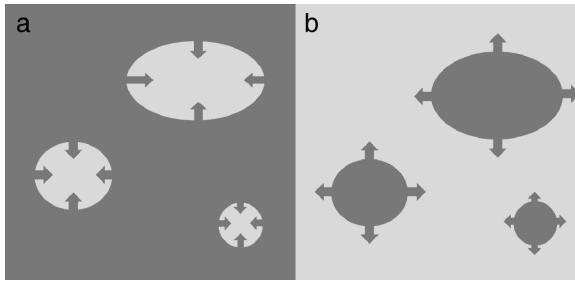


FIG. 1. Comparison between (a) open-gap dynamics where biotic matrix (dark gray area) is colonizing discrete, disturbed patches (light gray), and (b) remnant-patch dynamics in which remnant patches (dark gray) are colonizing largely disturbed, open landscapes.

(Levin and Paine 1974, Paine and Levin 1981). On rocky shores, for instance, herbivorous limpets accelerate mussel-bed recolonization when disturbances are small because limpets consume macroalgae that opportunistically settle in open patches and reduce interspecific competition (Sousa 1984). The positive effects of limpets are dampened in large disturbance patches, however, because limpets preferentially forage along the edge of mussel beds that provide a predation refuge, which allows macroalgae to proliferate in patch centers and stifle long-term recovery of mussel beds (Sousa 1984). In general, patch size-dependent shifts in the processes mediating community recovery arise because the internal area of disturbed patches scales nonlinearly with the length of the patch edge. This nonlinearity results in slower rates of recolonization via lateral spread of adults or propagules (Paine and Levin 1981) or neighborhood amelioration of physical stress (Bertness and Shumway 1993) from the adjacent community matrix as patches increase in size. Consequently, larger patches often take relatively longer to recover, or fail to recover fully, than do smaller ones (Sousa 2001).

In the contemporary context of remnant patches embedded within highly disturbed systems, size-dependent patterns in recovery are also likely. Small remnant patches, such as coral fragments that survive mass bleaching events, are likely to have proportionally more edge exposed to physical and biotic stressors and fewer stored resources to invest in expansion than larger patches (Okubo et al. 2007) due to the nonlinear relationship between patch edge and area. Thus, the resilience of remnant patches, specifically their ability to persist and expand after disturbance, is likely to be strongly size dependent. We predict that patch size-dependent processes will be important in mediating the rate of whole-community recovery in systems where foundation species, whose biotic structure modifies the physical environment and provides habitat for associated organisms (*sensu* Dayton 1972), exhibit clonal or positive density-dependent growth (e.g., corals after bleaching [Okubo et al. 2007], eelgrass in dredged seagrass meadows [Rasheed 2004], cordgrass in salt

marshes [Bertness and Shumway 1993]). Here, for the first time, we test the hypothesis that size of foundation species' patches influences their resistance to biotic and abiotic stress and recovery rate (i.e., in lateral expansion, growth, reproductive output) and explore the consequences of these patch-level dynamics for organisms dependent on the facilitative effects of foundation species following a major disturbance.

Salt marshes in the southeastern United States provide an ideal system to assess size-dependent recolonization processes. Over the past decade the synergistic effects of drought, snail grazing, and fungal infection have driven extensive losses of the foundation species, *Spartina alterniflora* (cordgrass), from marshes in this region (Silliman et al. 2005), leaving behind a mosaic of remnant grass patches embedded in an intertidal landscape dominated by mudflat and expansive monocultures of the succulent, long-lived perennial, *Sarcocornia* sp. (Fig. 2a). Because *Spartina* seedling establishment is extremely low in die-off areas (Travis and Hester 2005; this study), this mosaic of residual *Spartina* patches will likely provide the foundation and initial conditions for recovery of these ecosystems. In the absence of die-off, *Spartina* maintains a lush canopy along wave-protected shorelines, although its distribution and productivity are dynamically regulated by a combination of abiotic (i.e., tidal inundation, sediment composition, water availability) and biotic (i.e., top-down control, interspecific competition) factors (Pennings and Bertness 2001). Which of these factors most strongly affect small and large-patch growth and thus expansion rates remains unclear. In this study, we focused on three well-established plant-controlling factors in southern marsh ecosystems: water availability, consumer control, and interspecific plant interactions (Pennings and Bertness 2001, Silliman and Zieman 2001; see Plate 1).

On high-marsh platforms where *Spartina* die-offs were prevalent in the southeastern United States, intensive summer heat and solar stress can dry out the substrate and ramp up soil salinities to lethal levels in the absence of rain (Pennings et al. 2003). Thus, drought intensity is likely a key factor determining whether remnant patches shrink or expand. Similarly, snails that can reduce *Spartina* canopy structure by farming fungus in the wounds they create on live stems (Silliman and Zieman 2001) are extremely common in die-off marshes (Silliman et al. 2005) and may have disproportionately large effects on small remnant patches that have fewer belowground reserves to compensate for grazing damage than do larger patches. Additionally, *Sarcocornia* sp., which is typically restricted to high-marsh elevations, has invaded mid-marsh areas exposed when *Spartina* died back and often surrounds remnant *Spartina* patches (Fig. 2a). Whether *Sarcocornia* facilitates (via buffering evaporative stress, altering nutrient availability, and so forth) or inhibits (via competition for nutrients, space, or light) *Spartina* patch expansion is unknown and

offers an opportunity to evaluate the additional role of interspecific plant interactions in mediating remnant-patch dynamics.

Over two growing seasons that experienced high (2009) and low (2010) rainfall, we conducted a series of field experiments in Georgia (USA) salt marshes designed to test the individual, interactive, and patch size-dependent effects of drought stress (water availability), top-down control (snail grazing) and interspecific plant interactions (*Sarcocornia* presence) on *Spartina* recolonization. Given that a variety of ecosystems are experiencing similar massive disturbance events that wipe out much of the standing matrix of foundation species (e.g., global degradation of seagrass beds, Orth et al. 2006; mass coral bleaching, Alvarez-Filip et al. 2009; and hypoxia-induced die-off of benthic communities, Diaz and Rosenberg 2008), our results may provide general insight into long-term ecosystem resilience and inform future management of highly degraded habitats where enhancing the reestablishment of foundation species, and the organisms dependent on their facilitative effects, is of primary importance.

MATERIALS AND METHODS

Study area and community characteristics

All research was conducted within the National Estuarine Research Reserve on Sapelo Island, Georgia, USA (31°24'10.08" N, 81°17'3.84" W). Cumulative rainfall over the summer months (June–August [data source: Georgia Coastal Ecosystem LTER Data Catalog]) was 409 mm in 2009 and 274 mm in 2010—moderately wet and dry years, respectively, according to the Palmer Drought Severity Index (Appendix; data available online [State of Georgia, Division 9]).² To characterize abiotic conditions in die-off marshes, we measured soil moisture at low tide during a dry spell (six days without rain) as an integrative score of evaporative stress by calculating the amount of water retained in 4 cm diameter × 8 cm depth sediment cores collected in the three zones: *Spartina* (large patches), *Sarcocornia*, and unvegetated mudflat ($n = 10$ cores/zone; percentage soil moisture = water (g)/dry sediment (g)). We also repeatedly measured porewater salinity collected from 20 lysimeters that were inserted haphazardly throughout each zone over 2009 and 2010. To assess variation in faunal composition, we counted snails, mussels, and crab burrows identified to species (mud crab, *Sesarma* sp., and *Uca* spp.) in 24 50-cm² quadrats tossed haphazardly in each zone.

Spartina distribution surveys

To assess the regularity with which seedlings and patches of different sizes occurred in die-off areas and thus gauge their potential contribution to long-term

² <http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#>

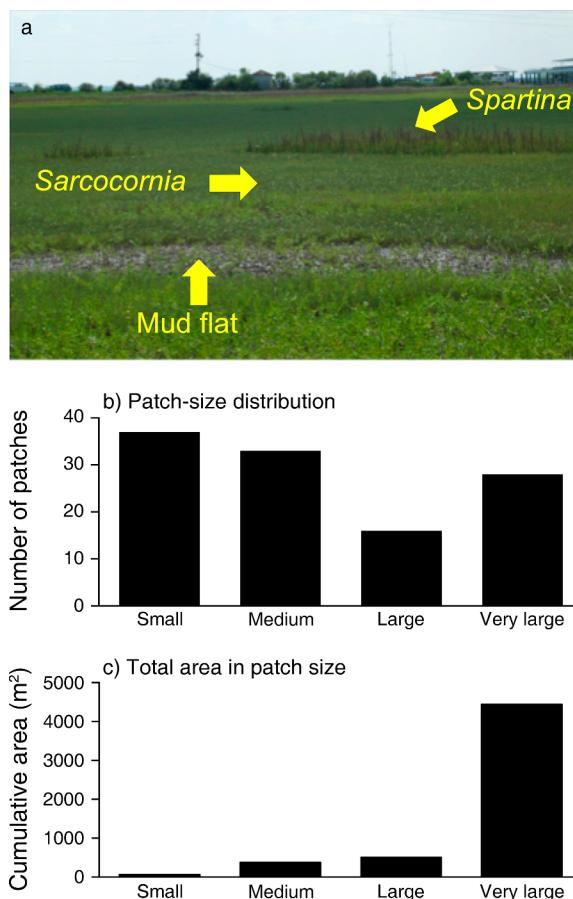


FIG. 2. Die-off marsh on Sapelo Island, Georgia, USA. (a) A 2009 photograph showing typical mosaic of *Spartina* patches, *Sarcocornia* monocultures, and mudflat (photo credit: C. Angelini). (b) Size-class distribution of *Spartina* patches within small (≤ 4 m²), medium (>4 –20 m²), large (>20 –50 m²) and very large (>50 m²) patches. (c) Total area of *Spartina* observed within each size class in transects conducted in three die-off marshes on Sapelo Island.

recolonization, we surveyed *Spartina* distribution at three marshes on Sapelo Island: Lighthouse, Marsh Landing, and Airport marshes, where extensive die-offs have occurred (Silliman et al. 2005). Along five 500-m transects within each marsh we quantified the number of *Spartina* seedlings observed within 0.5 m of each side of the transect tape and measured diameter and estimated total area of each *Spartina* patch we intersected. Transect data were pooled across marsh sites because seedling density and patch size distribution were similar.

Small-patch experiment

We tested the hypothesis that expansion and growth of small *Spartina* patches are mediated by *Sarcocornia* presence, snails, and drought stress (water availability) with a fully factorial transplant experiment conducted from June 2009 to April 2010. Over these 10 months, *Spartina* transplants progressed through one growth cycle in which new vegetative tillers grew to full terminal

stem heights. At Marsh Landing, 48 1-m² plots were randomly assigned one level of neighbor presence (*Sarcocornia* removal or neighbor control), snail treatment (snail exclusion cage or uncaged control), and water availability (addition or ambient water, $n = 6$ replicates per treatment). To minimize potentially confounding effects of sediment composition or other factors that may co-vary with the time since retreat of *Spartina* (see Paine and Levin 1981), we positioned plots 3 m from the boundary of remnant, very large (>50 m²) *Spartina* patches in the *Sarcocornia* matrix. Each plot received one *Spartina* transplant standardized for rhizome volume (30-cm³ blocks), stem height and density, collected from a nearby marsh relatively unaffected by die-off. To ensure that transplants established successfully, we set transplants flush with the marsh substrate, gently packed their sides with mud and monitored each daily for signs of stress, such as browning or wilting of leaves, for two weeks. We observed no signs of stress and all transplants generated new tillers within eight weeks. Transplants were used because there was significant variation in the elevation, faunal community composition, or *Spartina* stem height and density in natural small patches. One month prior to transplantation we applied a short-lived systemic herbicide to eliminate *Sarcocornia* from removal plots and weeded residual ramets as needed throughout the experiment (Bertness and Shumway 1993). Snails were excluded with 1-m³ roofless, galvanized mesh cages (1-cm mesh size) that were secured with wooden stakes and sunk 15 cm into the substrate. Every two weeks we plucked snails out of caged plots and the total number of snails removed never reached more than 5% of ambient levels. To manipulate water availability, 7 L of freshwater were applied evenly across 1-m² addition plots every other day from 10 July through 31 August and once per week until the end of September.

In April 2010 we quantified lateral expansion by counting all tillers >5 cm from the initial transplant boundary and measuring the maximum transplant diameter, the distance between the two furthest tillers. We then harvested transplants and scored each sample for stem height (eight random stems measured) and snail grazing intensity (total length of snail radulations on five random stems) and then oven-dried and weighed each to quantify the aboveground biomass.

Large-patch border movement

To evaluate the direction, rate, and variability of large-patch border movement, we established 70 plots over four marshes on Sapelo Island in June 2009 (30 plots at Airport, 20 plots at Dean Creek, 10 plots at Marsh Landing, and 10 plots at Lighthouse). On large *Spartina* patch–*Sarcocornia* borders, we marked 1-m² plots standardized for initial *Spartina* cover (32–40%) and inserted a reference flag next to the most advanced *Spartina* stem on each side of each plot. We monitored snail density, percent cover using a 100-cell string grid,

and distance between the stem most advanced in the *Sarcocornia* matrix and closest reference flag after one (April 2010) and two (August 2010) full growth cycles. To assess patch expansion, we calculated relative change in *Spartina* cover using: $(\% \text{Spartina}_t - \% \text{Spartina}_{\text{initial}}) / \% \text{Spartina}_{\text{initial}}$.

Large-patch border experiments

Because it was logistically infeasible to manipulate snails, *Sarcocornia* presence, and water availability on whole large-patch (>20 m²) scales, we focused on patch borders where we could measure expansion or retreat as a proxy for patch-level recolonization dynamics. To examine whether snails mediate large-patch border movement, we initiated a snail-removal experiment in May 2009. We haphazardly positioned 16, 1-m² plots along large *Spartina* patch borders (32–40% initial cover) where snail densities were moderately high (~225 snails/m²) and the adjacent *Sarcocornia* canopy of intermediate thickness (~28 cm high and 50% *Sarcocornia* cover; see the following paragraph for comparison). We excluded snails by using cages and by manual picking as above, and severed belowground plant connections around control plots to standardize the effects of cage installation ($n = 8$ plots per treatment). In April 2010 we scored *Spartina* cover, calculated relative change in cover and harvested aboveground plant material from 30-cm² quadrats in each plot to assess snail effects on canopy structure. Samples were sorted to species and *Spartina* stem height and dry aboveground biomass were quantified as above.

To evaluate whether neighbor presence influences border movement of large *Spartina* patches, we set up *Sarcocornia*-removal experiments at Airport and Marsh Landing, where surveys of *Sarcocornia* stem height (in centimeters) and percentage cover revealed neighbor canopy to be relatively sparse and dense (height = 23.0 ± 1.2 cm and 31.1 ± 1.1 cm, respectively, and cover = $30.4\% \pm 4.8\%$ and $70\% \pm 9.2\%$ [mean \pm SE] in 10, 50-cm² survey quadrats haphazardly tossed in *Sarcocornia* monocultures at each site). On large *Spartina* patch–*Sarcocornia* borders (32–40% cover *Spartina*), we demarcated 20, 1-m² plots at each site and randomly assigned each a *Sarcocornia* removal or control treatment ($n = 10$ plots per treatment). We weeded *Sarcocornia* from removal plots monthly and collected percent cover data in April and August 2010, after the 2009 and 2010 growth cycles.

Because drought stress might influence *Spartina* patch dynamics directly through water limitation or indirectly by elevating soil salinities, we modified our methods from the small-patch experiment, where we only added freshwater, in the large-patch experiment by adding both water (to alleviate the direct effect of water limitation) and salt (to mimic a major indirect effect of water limitation) to large-patch borders to test for their independent effects on patch dynamics. In June 2010 we demarcated 24, 50-cm² plots along borders between

TABLE 1. Summary of abiotic and biotic conditions in three zone types on Sapelo Island (Georgia, USA) marshes impacted by die-off.

Zone type	Abiotic conditions		Biotic abundance (no./m ²)				
	Porewater salinity (ppt)	Soil moisture (water mass/sediment mass)	Snails	Mussels	Mud crab burrows	<i>Uca</i> burrows	<i>Sesarma</i> burrows
<i>Spartina</i>	37.7 ^b (0.8)	1.88 ^a (0.13)	225 ^a (27)	1.17 ^a (0.40)	1 ^a (0.31)	10.3 ^b (0.99)	2.83 ^a (0.73)
<i>Sarcocornia</i>	51.7 ^a (1.3)	1.46 ^b (0.04)	90 ^b (11)	0.25 ^b (0.09)	0.13 ^b (0.09)	17.6 ^a (2.98)	0 ^b (0)
Mudflat	48.4 ^a (1.1)	1.46 ^b (0.03)	14 ^c (3)	0.17 ^b (0.10)	0.42 ^{a,b} (0.17)	6.5 ^b (0.69)	0.04 ^b (0.04)
<i>P</i>	<0.0001	0.0012	<0.0001	0.0086	0.0141	0.0002	<0.0001

Notes: Data are means with SE in parentheses. Results from Tukey's post hoc analysis are indicated by lowercase letters next to means—different lowercase letters indicate significant differences at $P = 0.05$. Significance values from marsh zone ANOVA are shown in the last line.

large *Spartina* patches (32–40% initial cover) and unvegetated mudflat, reference-flagged the most advanced tillers as above, and randomly assigned either a salt-addition, water-addition, or control treatment to each. We placed 8, 50-mL centrifuge tubes, filled with Instant Ocean Sea Salt (Spectrum Brands, Madison, Wisconsin, USA) and drilled to allow salt to diffuse passively into the substrate in salt-addition plots, and placed eight empty, drilled tubes in control and water-addition plots as procedural controls (Silliman et al. 2005). Salt tubes were refilled as needed. Due to a prolonged midsummer drought, water-addition plots received 7 L of water per day on every odd-numbered day in June, daily from 16 July through 18 August 2010, and again on every odd-numbered day thereafter until 31 August. In early September we measured the distance between the closest reference flag and the most advanced tiller, and counted the total number of inflorescences and stems in each plot. We then harvested all stems within a 30-cm² quadrat placed in the center of each plot, measured the height of eight random stems, and then oven-dried and weighed each sample.

Statistical analysis

Data were analyzed with JMP 8.0 (SAS Institute 2009). Differences among treatments in the small-patch experiment were assessed with three-way (snail \times neighbor \times water) ANOVA. For large-patch monitoring data, we used repeated-measures ANOVA to evaluate the effect of marsh site on variation in border movement over 2009 and 2010 growth cycles. Linear regression was used to investigate the relationship between average snail density and relative change in *Spartina* cover in large-patch monitoring plots. For the large-patch manipulative experiment data, we assessed the effect of snail removal or drought stress (water availability) treatment on *Spartina* growth and the relative change in cover using single-factor ANOVA. For the neighbor-removal experiment we nested neighbor treatment within site to account for site-specific differences in *Sarcocornia* canopy (sparse and dense) and used repeated-measures ANOVA. Response parameters were log-transformed as necessary to comply with parametric assumptions and post hoc analyses were by Tukey's hsd.

RESULTS

Abiotic and biotic characteristics of *Spartina*, *Sarcocornia*, and mudflat

Results from the 70 plots we established over four marshes on Sapelo Island, Georgia, USA, showed that across die-off marshes there were persistent differences in abiotic and biotic conditions between remnant *Spartina* patches, *Sarcocornia* monocultures, and unvegetated mudflat (Table 1). Soil moisture was significantly higher and salinity significantly lower in *Spartina* relative to both *Sarcocornia*-dominated areas and mudflats. Snails, mussels, mud crabs, and *Sesarma* were also far more abundant in regions still colonized by *Spartina*, although snails persisted in moderate densities in *Sarcocornia* as well (~ 100 snails/m²). Fiddler crab burrows, by contrast, were 2 times higher in *Sarcocornia* than in mudflat or *Spartina* (Table 1).

Spartina distribution surveys

In die-off areas, *Spartina* seedlings were rare (24 seedlings per 500-m² survey transect on average) and often clustered near the high-marsh border rather than spread broadly throughout the marsh. Thus, most of the *Spartina* was found in remnant patches that varied greatly in size. We observed a relatively equal number of patches in all size categories (Fig. 2b), although an overwhelming proportion of the *Spartina* remaining was in large, rather than small, patches (Fig. 2c).

Small-patch experiment

Removing plant neighbors and snails revealed that small patches are strongly limited by both *Sarcocornia* and top-down control (Fig. 3). The presence of *Sarcocornia* stifled the expansion of small *Spartina* transplants: when *Sarcocornia* was removed, transplants showed mean increases in expansion tiller density and maximum diameter of 235% and 166%, respectively (Fig. 3a, b; neighbor, $F_{1,40} \geq 67.16$, $P < 0.0001$). Snail removal, which effectively reduced grazing intensity on small patches (snail, $F_{1,40} = 70.35$, $P < 0.0001$), also prompted a 133% increase in *Spartina* stem height (snail, $F_{1,40} = 101.15$, $P < 0.0001$; Fig. 3c). Aboveground biomass, an integrative measure of both lateral and

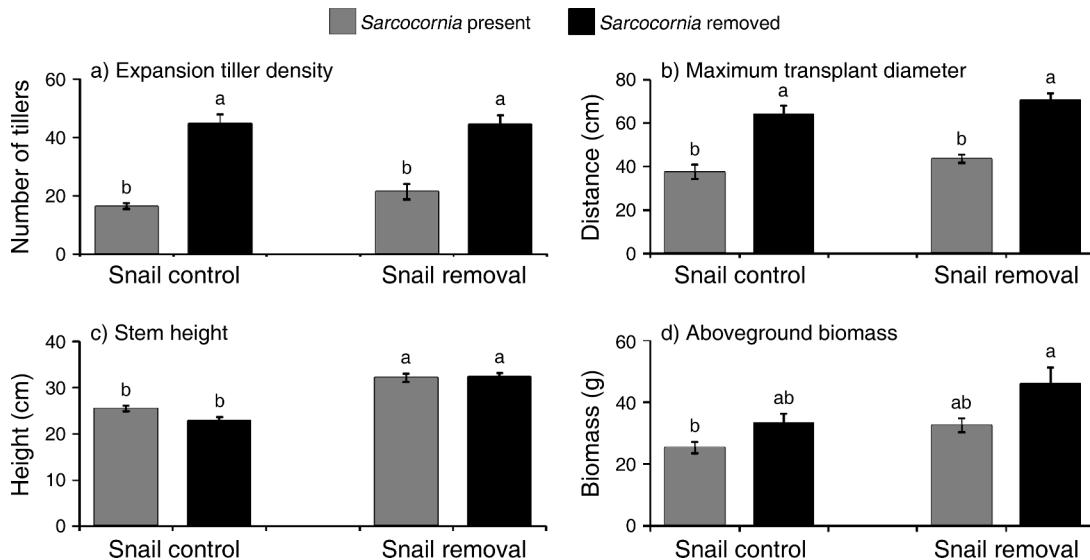


FIG. 3. Effect of neighbor (*Sarcocornia*) and snail removal on small *Spartina* patches, averaged across water treatments as there was no statistically significant effect of watering. Data are means \pm SE; different lowercase letters above the bars indicate a significant difference at $P = 0.05$ (results from Tukey's post hoc analyses).

vertical plant growth, revealed that neighbor presence and snails additively suppress small patches (neighbor: $F_{1,40} = 9.52, P = 0.0037$; snail, $F_{1,40} = 8.05, P = 0.0071$; Fig. 3d). By contrast, watering had little effect on transplant growth ($F_{1,40} \leq 1.38, P \geq 0.2460$).

Large-patch border movement

Large-patch borders advanced over the first growth cycle that coincided with the moderately wet summer and fall of 2009, with *Spartina* cover increasing by an average of $20.8 \pm 1.5\%$ across all sites (mean \pm SE; Fig. 4a). During the second year when conditions were substantially drier we detected site-specific variation in border movement at the four marsh sites, with borders continuing to expand at Airport, but stabilizing or slightly retracting at Lighthouse, Dean Creek, and Marsh Landing marshes (time \times site: Wilks' $\lambda = 0.614, P < 0.0001$; Fig. 4a). Despite their influence on the

initial die-off of *Spartina* (Silliman et al. 2005), we found no relationship between mean snail density and the relative change in *Spartina* cover in either the 2009 or 2010 growth cycle (Fig. 4b) or cumulatively over the experiment ($R^2 \leq 0.005, P \geq 0.5576$).

Large-patch manipulative experiments

Removing snails had a negligible effect on the change in cover, aboveground biomass, or stem height of *Spartina* ($F_{1,14} \leq 1.39, P \geq 0.2580$), providing further evidence that snails did not significantly mediate large-patch border movement. In the plant-neighbor experiment, however, we found that *Spartina* advanced significantly more where *Sarcocornia* was removed, but only during the drier, second year and only at Marsh Landing where the *Sarcocornia* canopy was dense (time \times treatment [site]: Wilks' $\lambda = 0.430, P < 0.0001$; Fig. 5). Finally, watering large-patch borders during the rela-

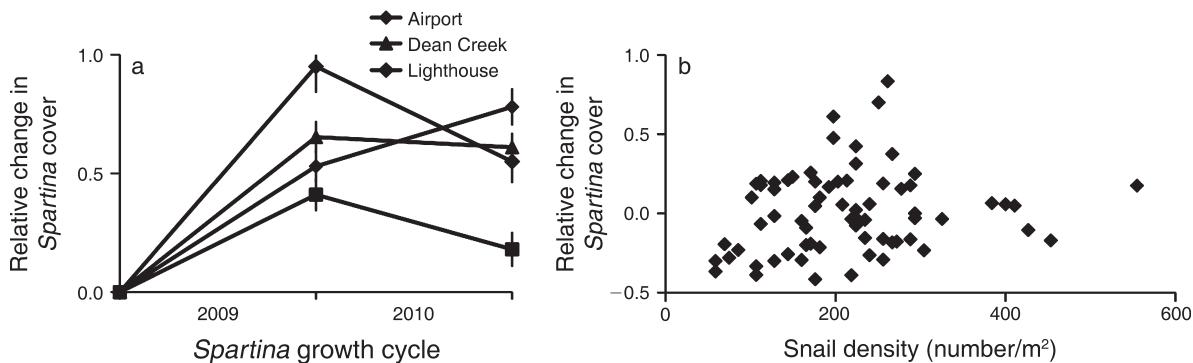


FIG. 4. (a) Relative change in *Spartina* cover in large-patch border plots monitored over 2009 and 2010 in four marshes on Sapelo Island, Georgia, USA. Data are means \pm SE. (b) The relationship between average snail density and the change in *Spartina* cover in ambient border plots in 2010.

tively dry summer of 2010 elicited a strong positive response: maximum tiller distance increased by 292% ($F_{2,21} = 4.42$, $P = 0.0249$), aboveground biomass by nearly 200% ($F_{2,21} = 25.32$, $P < 0.0001$), stem density by 33% ($F_{2,21} = 5.98$, $P = 0.0088$), stem height by 186% ($F_{2,21} = 43.25$, $P < 0.0001$), and inflorescence density by 430% ($F_{2,21} = 5.26$, $P = 0.0141$) compared to salt addition or controls. Salt-addition plots were similar to controls in all plant growth metrics, and salinity measurements taken throughout the summer indicated that salt addition had negligible effect on porewater salinity. This treatment failure was likely due to persistent dryness of the substrate that prevented salt from leaching from diffusion tubes.

DISCUSSION

These findings provide the first explicit experimental evidence for patch size-dependent community recovery in southeastern U.S. marshes following massive drought–grazer disturbance. Our results revealed that *Spartina* transplants expanded little unless plant neighbors and snail grazers were removed, suggesting biotic inhibition will prevent small, lingering grass patches from contributing significantly to marsh recovery over the long term. *Spartina* in large patches, by contrast, successfully advanced into die-off areas in the wetter 2009 season and demonstrated resistance to grazing and plant neighbors during more stressful drought conditions in 2010. Thus, the size distribution of remnant patches, as well as the duration of favorable growth periods and the frequency and intensity of stressful events (i.e., drought, heat waves, consumer outbreaks), are likely to play a pivotal, interactive role in determining ecosystem resilience and the pace at which foundation species and their associated communities can recover after massive disturbance.

Size-dependent recovery

We found that the importance of abiotic stress and species interactions shifted as remnant patches increased in size, a result that echoes size-dependent patterns described earlier for open-gap dynamics (Sousa 1984, Bertness and Shumway 1993). Relative to their internal area, small patches maintain an extensive interface with the external environment where, in marsh die-off areas, the soils are drier and saltier and the faunal community that performs key ecosystem functions, such as substrate aeration, sediment turnover, and nutrient cycling, is depauperate (Table 1). Even over the rainy growing season in 2009, a period of relaxed physical stress when we would expect *Spartina* to exhibit vigorous growth, small experimental patches barely expanded into adjacent areas unless plant neighbors were removed (Fig. 3a, b). This response suggests interspecific interference plays a key role in restricting small-patch expansion. In addition, snails rapidly congregated on *Spartina* transplants, particularly where *Sarcocornia* provided a canopy conduit for snail migration (C. Angelini, unpublished data).

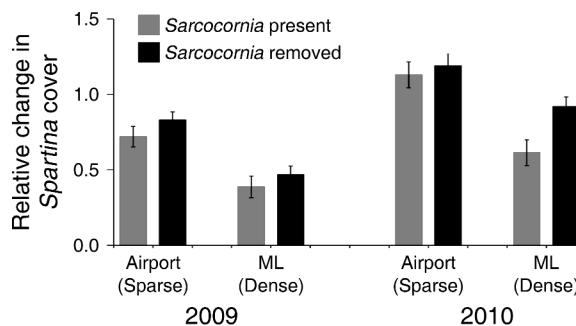


FIG. 5. Effect of neighbor removal on the relative change in *Spartina* cover at Airport and Marsh Landing (ML) marshes in 2009 and 2010. Data are means \pm SE.

As an unpalatable neighbor (R. McNulty, unpublished data), *Sarcocornia* appears to concentrate grazers on more palatable, isolated *Spartina* patches, thus intensifying consumer pressure and compromising plant growth (Alberti et al. 2008). Intensive grazing is known to induce structural and chemical defenses in *Spartina* and many other vascular plants (Long et al. 2011), which may reduce resource allocation to growth, and, in the context of remnant patches, further limit the ability of individual patches to expand. Overall, these findings suggest that the presence of early successional species, like *Sarcocornia* in southeastern U.S. salt marshes or weedy, invasive algae in disturbed seagrasses (Orth et al. 2006), can exacerbate physical and biotic stress along patch edges and interfere with the vegetative expansion of small, foundation-species patches.

By contrast, large-patch expansion was sensitive to water availability and only affected by one species interaction (plant neighbors, not grazing) under drought conditions when competition among plants, most likely for water, intensified (Figs. 4, 5). This temporally and spatially heterogeneous response of large-patch borders to neighbor removal suggests that the strength of interspecific plant interactions may be both drought and density dependent. Drought dependence seems likely driven by the higher drought tolerance of *Sarcocornia* (Pennings et al. 2003) and density dependence could result from *Sarcocornia* monocultures with thicker canopies and more prolific root networks interfering with *Spartina* tiller expansion and growth more effectively than sparser, less prolific monocultures. The positive response of *Spartina* borders to watering provides additional experimental evidence that water availability (moderated by drought) can regulate the rate and pattern of growth of *Spartina* in die-off landscapes. The correlation we observed between moderate physical stress and patch expansion indicates that the incidence of environmental conditions that favor the growth of foundation species, such as mild storm seasons in degraded mangroves (Alongi 2008) or periods of improved water clarity in disturbed seagrass meadows (Orth et al. 2006), will play a crucial role in determining whether these ecosystems will recover naturally from



PLATE 1. (a) *Spartina* die-off area in Airport Marsh on Sapelo Island, Georgia, USA, where *Sarcocornia* sp. is invading the high marsh platform and surrounding remnant patches of *Spartina alterniflora*. (b) Close-up of the pickleweed, *Sarcocornia*, and (c) the periwinkle snail, *Littoraria littorea*, grazing on fungal infected wounds on *Spartina*. Photo credits: (a, b), C. Angelini; (c) B. R. Silliman.

massive disturbance, because it is primarily during these favorable intervals that large foundation-species patches effectively outcompete other, functionally inferior space holders and reestablish dominance.

In contrast to their suppressive effect on small patches, grazers had a negligible influence on the movement or canopy structure of large-patch borders (Figs. 4b, 5). This result is primarily explained by the density of snails in and along the edges of patches that became highly concentrated on small patches (mean density throughout experiment: 896 ± 70 individuals/ m^2) compared to large patches (213.6 ± 11.6 ind./ m^2). In fact, snail densities only exceeded the projected threshold for grazing-induced canopy degradation of *Spartina* (~ 500 ind./ m^2) on small patches (see Silliman et al. [2005] for discussion). This difference in grazer density in

small vs. large patches may be partially explained by patterns in behavior and movement of snails that migrate into and forage within large and small patches. Due to the spatial extent of large patches, grazers can readily migrate away from high densities of conspecifics where preferred food resources (senesced or fungal-infected stems) may be depleted to regions with fewer conspecifics and more abundant resources, resulting in a diffusion of top-down impacts on large-patch edges where *Spartina* expansion occurs. In small patches, in contrast, snails tend to accumulate because individuals that attempt to migrate away from conspecifics quickly encounter either mudflat (little food or refuge) or *Sarcocornia* (less palatable food) and likely return to the patch. Consequently, natural immigration of grazers with limited mobility, like snails, into small remnant

patches appears to concentrate their densities and intensify their top-down impacts on foundation species and could potentially lead to patch extinction over time.

Additionally, the ambient snail densities we observed during this study (range, 58–554 snails/m²; Fig. 4b) were generally lower than during the die-off period (400–2000 snails/m²; Silliman et al. 2005), suggesting large-scale and long-term drivers of grazer population dynamics may also be important to consider in recovery predictions. Specifically, blue crabs (*Callinectes sapidus*), common snail predators, are strongly suppressed during drought years, which may precipitate large fluctuations in adult snail densities and, thus, their potential grazing impact (B. R. Silliman, M. Hensel, J. Nifong, S. van Montfrans, R. McNulty, and C. Kennedy, *unpublished manuscript*). Since the initial large-scale 1999–2001 die-off in these marshes there have been a few wet years and subsequent recovery of blue crabs, potentially leading to lower densities of plant-grazing snails and thus dampened top-down control on plants (B. R. Silliman, M. Hensel, J. Nifong, S. van Montfrans, R. McNulty, and C. Kennedy, *unpublished manuscript*). Although we cannot currently infer how trophic dynamics might contribute to overall ecosystem resilience as further analyses are needed, our results do point to an interesting conclusion regarding snail impacts alone: the spatial scale at which grazers act to drive ecosystems to collapse (very large, whole-marsh landscapes, Silliman et al. 2005) is very different from the scale at which they impact recovery (small-patch scales; this study).

Succession in highly disturbed marsh landscapes

In southern marshes experiencing die-off, we found evidence for inhibitive succession in which the establishment of *Sarcocornia* has hampered *Spartina* recolonization. This pattern contrasts with that found in New England where plants that first colonize disturbance patches facilitate the return of clonal marsh dominants and accelerate recovery (Bertness and Shumway 1993). Since marsh recovery rates could differ significantly under inhibitive and facilitative succession, it is important to understand what mechanisms underlie discrepancies in the strength of interactions between early- and late-successional species across latitudes. One reason may be constitutive differences in physical stress tolerance between northern and southern marsh plant communities (Pennings et al. 2003). In New England where summers are often short and moderate, the dominant, turf-forming plants rarely experience water or salinity stress and, therefore, depend on the ameliorating effects of stress-tolerant species to return to dry, hypersaline bare patches generated by wrack and ice (Bertness and Ewanchuk 2002). By contrast, in southern marshes where summers are longer and hotter, plants are locally adapted to variable water and salinity conditions and thus more tolerant of drought stress (Pennings et al. 2003) and potentially less dependent on the stress-ameliorating effects of early successional

plants to recolonize disturbance patches. Instead, they may compete with rapid colonizers for limiting resources. Consequently, both current environmental conditions and historic physical or biological stress regimes likely influence whether inhibitive or facilitative interactions primarily regulate succession in disturbed systems, where foundation species must replace weedy colonizers to reestablish spatial dominance and restore ecosystem functioning.

*Community-level consequences of *Spartina* recovery*

Our surveys show that *Spartina* maintains a far richer faunal community than either *Sarcocornia* or unvegetated mudflat (Table 1). Mud crabs (*Panopeus herpsthii* and *Eurythium limosum*), which are common sit-and-wait predators that affect snail abundance and behavior (Griffin and Silliman 2011), marsh crabs (*Sesarma reticulatum*) that excavate extensive burrow networks, and snails and mussels that drive detrital food webs and nutrient cycling (Silliman and Ziemann 2001) all occurred at densities 1.5–3 times higher in *Spartina*. This suggests that the spatial distribution of faunal assemblages is contracted when *Spartina* is reduced, regardless of the presence of *Sarcocornia*, and will increase only with the successful expansion of *Spartina* patches. Although facilitation of higher trophic-level organisms by spatially dominant, highly productive foundation species, like *Spartina*, is common to many ecosystems (Bruno et al. 2003), our current understanding of how associated communities reestablish along with these key, habitat-forming species after disturbance remains limited and would certainly benefit from further research.

Climate change and the future of southeastern U.S. marshes

In the face of climate change and intensive human modification of natural landscapes, the frequency and intensity of disturbance events are projected to increase over coming decades (e.g., Folke et al. 2004, Orth et al. 2006). Understanding whether organisms, their interactions and the services they provide can persist under such disturbance regimes requires that we understand the processes mediating their resilience. This study suggests that efforts to restore highly disturbed ecosystems should primarily focus on retaining relatively large habitat patches that have a higher level of resilience to both local biotic interactions and the ongoing intensification of climatic conditions. In particular, protecting large patches of foundation species, which provide biotic structure, food, and refuge for other organisms (Dayton 1972), will not only promote natural-habitat recovery, but also the recovery of the dependent communities and ecological services they provide. Additionally, in ecosystems where disturbance events have left remnant patches too small to overcome size thresholds or vast expanses between large-patch boundaries, successful restoration strategies will likely be those that establish large patches through transplantation or propagule

additions that can sustain themselves over time. These results emphasize the important role patch size plays in mediating recovery and suggest that communities will not linger in degraded states if patches that are left are large enough to support associated organisms, exhibit positive growth during favorable environmental conditions, and resist biotic inhibition.

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SUPPLEMENTAL MATERIAL

Appendix

A figure presenting southeastern U.S. region precipitation, temperature, and drought-severity levels in 2009 and 2010 (*Ecological Archives* E093-010-A1).