

# Whether disturbances alter salt marsh soil structure dramatically affects *Spartina alterniflora* recolonization rate

SEAN J. SHARP<sup>†</sup> AND CHRISTINE ANGELINI

Department of Environmental Engineering Sciences, Engineering School for Sustainable Infrastructure and Environment,  
University of Florida, Gainesville, Florida 32611 USA

**Citation:** Sharp, S. J., and C. Angelini. 2016. Whether disturbances alter salt marsh soil structure dramatically affects *Spartina alterniflora* recolonization rate. *Ecosphere* 7(11):e01540. 10.1002/ecs2.1540

**Abstract.** Disturbance regimes are shifting in response to climate change, land-use change, species' invasions, and other stressors, challenging ecologists to improve understanding of the mechanisms controlling plant recovery under different conditions. In this study, we investigate mechanisms that underpin plant recolonization of two types of disturbance: disturbances that remove standing plant biomass, but leave the underlying soil structure largely intact, and those that remove standing biomass and physically disrupt soil structure. In the southeastern United States, salt marshes, drought and invasive feral hogs (*Sus scrofa*) are associated with disturbances of these respective types and both leave behind mudflats dotted with patches of cordgrass (*Spartina alterniflora*), the system's dominant foundation species. To test how disturbance type and remnant patch size may interact to affect cordgrass recolonization, we transplanted replicate cordgrass patches of three sizes into one mudflat that experienced vegetation-only disturbance (VD) during a recent drought, and a second mudflat where hog activities had disrupted the soil structure creating a soil + vegetation disturbance (soil + VD). Over one year, we monitored plant performance and properties of soil. Compared with the drought-associated VD where patches, regardless of their size, expanded vigorously, large and medium patches grew little and smaller patches even less in the hog-associated soil + VD mudflat. Moreover while biogeochemical properties varied little in the VD compared with adjacent vegetated marsh areas, the mudflats with soil + VD had less soil-binding organic matter and, hence, were too soft to support crab burrows, leading to a reduction in oxygen availability and cordgrass expansion. These results indicate that cordgrass recovery is far faster from disturbances that do not degrade soil structure than those that do and therefore advocate for disturbance-specific management strategies. Specifically, while transplanting patches is effective in restoring marshes disturbed by drought, wrack, or other factors that leave soil structure intact, preventative measures, like hog population culling, are essential to mitigating the ecological impacts of soil structure-altering disturbances.

**Key words:** biogeochemistry; drought; ecosystem engineers; foundation species; invasive species; resilience; restoration; *Sus scrofa*; wetland.

**Received** 6 September 2016; accepted 7 September 2016. Corresponding Editor: Debra P. C. Peters.

**Copyright:** © 2016 Sharp and Angelini. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

<sup>†</sup> **E-mail:** seanjsharp@ufl.edu

## INTRODUCTION

Disturbances, such as droughts, storms, wildfires, and tree falls, have long been recognized as important drivers of ecosystem structure and function both through their initial removal of plants, animals, and resources and through their

subsequent stimulation of community recovery and succession (Sousa 1979, White 1979, Mouillot et al. 2013). In terrestrial systems, disturbances of different types, intensities, and scales vary in the extent to which they influence abiotic conditions and the distribution of surviving plants, factors that then moderate the rate of ecosystem

recovery to predisturbed states (Johnson and Miyanishi 2007). Although a number of prior studies have shown that disturbance attributes and surviving plant characteristics each are important factors regulating ecosystem resilience and recovery (Halpern et al. 1990, Angelini and Silliman 2012, Altieri et al. 2013, Gustafsson and Boström 2013), none to our knowledge have manipulated surviving plant patch size within multiple types of disturbance to test how these factors may interact to control the rate of vegetation recovery. Elucidating whether, and why, different patch sizes of surviving plants may exhibit unique recolonization rates is important for informing the design of management and restoration strategies for disturbed, low-functioning ecosystems.

Salt marshes are intertidal wetlands that form along low-energy, temperate coastlines where they provide a number of valuable ecosystem services (Beck et al. 2001, Zedler and Kercher 2005, Barbier et al. 2011). Because a variety of natural and anthropogenic disturbances are increasingly threatening the provisioning of these services, salt marshes are an important system for testing how disturbance type may interact with the patch size of surviving plants to control the pattern and rate of ecosystem recovery (McKee et al. 2004, Alber et al. 2008, Cardoni et al. 2011, Wasson and Woolfolk 2011, Coverdale et al. 2014, Angelini et al. 2016). Within salt marshes, disturbances vary in their spatial extent and in the size of remnant patches they leave behind. For example, droughts that interact with snail grazer facilitation of fungi can wipe out expansive areas (100s–1000s of m<sup>2</sup> of marsh) and leave behind a mosaic of grass patches that vary widely in size (Silliman et al. 2005, Angelini and Silliman 2012, Angelini et al. 2016). In addition, different types of disturbance uniquely impact marsh soil biogeochemistry, sediment grain size composition, and resident fauna, and these factors can mediate subsequent marsh recovery (De Leeuw et al. 1992, Allison 1996, Tolley and Christian 1999, Wall and Virginia 1999). As disturbed marshes are susceptible to drowning via soil erosion and subsidence when soil-stabilizing grasses do not recover quickly (Christie et al. 1999, Day et al. 2011, Voss et al. 2013), understanding the mechanisms that control grass recolonization after different disturbances has important implications

for the management and long-term stability of this valuable coastal ecosystem. In addition, identifying whether there is pronounced seasonality in patch lateral expansion and stem production is important for informing managers of when to transplant grass and monitor restoration success (Odum and Smalley 1959, Odum et al. 1995).

In the southeastern United States, smooth cordgrass, *Spartina alterniflora* Loisel (hereafter cordgrass), dominates low and intermediate salt marsh elevations and functions as this system's foundation species (Morris et al. 2002, Angelini et al. 2015). Over recent decades, severe droughts have been causally linked to loss of well over 100,000 ha of cordgrass in salt marshes distributed from coastal Louisiana to South Carolina (McKee et al. 2004, Silliman et al. 2005, Alber et al. 2008; Fig. 1a, c). These events kill cordgrass and, in removing its standing stems but leaving its roots and rhizomes in place, create denuded mudflats characterized by fairly firm, intact substrates. Invasive feral hogs (*Sus scrofa*) also disturb salt marshes through their trampling, rooting, and wallowing activities, actions that both remove standing cordgrass and significantly disrupt the underlying soil structure (Fig. 1b, d; Wood and Brenneman 1980, Ford and Grace 1998, Herrero et al. 2004, Bracke 2011). Recolonization of *Spartina* spp. in disturbance mudflats is primarily achieved through clonal expansion of surviving cordgrass patches rather than seed dispersal (Hartman 1988, Proffitt et al. 2003, Travis and Hester 2005, Mateos-Naranjo et al. 2008, Angelini and Silliman 2012). Due to differences in belowground energy reserves, intraspecific competition, and intraspecific facilitation, cordgrass clonal expansion is known to vary with patch size and environmental conditions (Pennings and Callaway 2000, Angelini and Silliman 2012). Prior studies have estimated recovery time either after disturbances that remove vegetation (Bertness and Ellison 1987, Pennings and Callaway 2000, Angelini et al. 2016) or after disturbances that remove vegetation and later experience a shift in soil properties (e.g., geese grubbing: Jefferies et al. 2006). Due to the lack of direct comparisons between disturbance types, it remains unclear how different recolonization rates might be in vegetation-only disturbances (VDs) vs. soil + vegetation disturbances,



Fig. 1. Landscape (a, b) and bird's eye view (c, d) of disturbances that remove vegetation but leave soils intact (right panels) and those that physically disrupt soil structure in addition to removing vegetation (left panels) in southeastern salt marshes. Photograph credit: C. Angelini (a) and S. Sharp (b–d).

and whether patch expansion in these different contexts depends on initial patch size.

Here, we present results from a year-long field experiment in which we tested the effects of patch size and disturbance type (i.e., VD and soil + VD, hereafter simply “VD” and “S + VD”) on cordgrass recovery. We hypothesized that (1) due to their access to larger belowground energy reserves to allocate to clonal growth, large patches would expand across mudflats at a faster rate and produce more biomass (measured in terms of both relative and total biomass production) than smaller patches in both VD and S + VD mudflat types. However, (2) while intraspecific facilitation would allow large patches to continually grow faster than smaller patches in the physically harsher, S + VD mudflat, intraspecific competition in large patches and the gradual accumulation of belowground energy reserves in smaller patches would result in similar growth of patches of all sizes over time in VD mudflats. And, finally, we predicted that

(3) patches of all sizes would grow and expand significantly less within S + VD mudflats, due to lower oxygen availability in the soil, relative to VD mudflats.

In this study, drought-associated stresses created the VD mudflat where the soil structure was firm as analysis of aerial images indicates its formation coincided with the most recent severe drought in the region and it was vegetated prior to this event (Angelini and Silliman 2012, NOAA U.S. Climatic Data Georgia division 9, [http://www.cpc.ncep.noaa.gov/products/monitoring\\_and\\_data/drought.shtml](http://www.cpc.ncep.noaa.gov/products/monitoring_and_data/drought.shtml)). Likewise, invasive hogs contributed to the formation, or at least maintenance, of the S + VD mudflat where the soil structure was substantially altered relative to adjacent vegetated marsh areas (e.g., the rhizome mat was broken up and exposed) and there was regular evidence of hogs, including fresh wallows, scat, and hoof prints, around the site over the course of the study (although no direct hog disturbance was ever recorded within study plots). Although

we focus on drought- and hog-generated mudflats, we anticipate that our findings have general relevance to other common types of salt marsh VDs, like wrack deposition, and S+VDs, such as invasive nutria, geese grubbing, and burrowing marsh crab consumer fronts.

## MATERIALS AND METHODS

### Study site

We examined recovery of cordgrass in VD and S+VD mudflats within the Sapelo Island National Estuarine Research Reserve on Sapelo Island, Georgia, United States (31°24'27" N, 81°17'27" W and 31°26'58" N, 81°14'22" W, respectively) from September 2013 to September 2014. The salt marshes on Sapelo Island are representative of those throughout the southeastern Atlantic U.S. coast as they are dominated by cordgrass at low and intermediate tidal elevations and by common marsh succulent plants and shrubs at higher elevations (Pennings and Bertness 1999, Pennings et al. 2012). The S+VD was located on the northeast side of Sapelo Island within a Georgia Department of Natural Resource wildlife management area that supports a robust hog population, while the VD was located 6.2 km away on the southwestern side of the island where hogs are far less commonly observed (Will Ricks, GA DNR, *personal communication*). Both mudflats were between 400 and 500 m<sup>2</sup>, dotted with a few surviving cordgrass patches (initial patch size: 0.01–0.2 m<sup>2</sup> and 5–30 stems), and surrounded by expansive cordgrass monocultures. We set reference plots within cordgrass monocultures that were at the same elevation as, and within 50 m of each mudflat but out of the affected area.

To assess the duration of tidal inundation at each site, a factor that may mediate cordgrass growth (Voss et al. 2013), we used a groundwater piezometer equipped with pressure transducers to record the water level every 15 minutes (Solinst level logger), corrected these data for fluctuating atmospheric pressure (data from the Sapelo Island National Estuarine Research Reserve Marsh Landing meteorological station, [www.cdmo.baruch.sc.edu](http://www.cdmo.baruch.sc.edu)), and combined these data with elevation measurements taken from each site using a Centerpoint RTK GNSS Receiver with real-time accuracy corrections (Trimble, Sunnyvale, California, USA).

### Effects of patch size and disturbance type on cordgrass recovery

To test the effects of patch size and disturbance type on the rate of cordgrass recovery, we transplanted cordgrass patches of three size classes (small, medium, and large representing a range of sizes typically observed in individual patches within both disturbed areas, Angelini et al. 2016 and S. Sharp, *unpublished data*) in both the VD and S+VD sites. All patches were positioned >1 m apart and >3 m from cordgrass positioned within or around mudflat areas. Due to the differences in VD and S+VD total mudflat areas used in this study and to standardize the density of transplants within disturbance areas, we transplanted fewer replicates at the S+VD than at the VD site ( $N = 6$  and  $N = 16$  patches per size class, respectively). At each site, we used PVC corers to extract transplants, standardized for initial stem height and health as well as core depth (15 cm), from well-vegetated, although heterogeneously clumped, cordgrass stands adjacent to the disturbance mudflat at each site. Patches of each size class differed in their number of stems (small:  $3.4 \pm 0.16$ , medium:  $8.3 \pm 0.33$ , large:  $13.7 \pm 0.36$ , mean  $\pm$  SE) and volume of soil and root material (small: 100 cm<sup>3</sup>, medium and large: 250 cm<sup>3</sup>).

To account for seasonal variability in environmental conditions and in transplant lateral expansion and growth rates, we monitored the expansion area, density, and stem height of each patch approximately once per month for 12 months. We measured the distance between outermost ramets along two fixed orthogonal axes within each plot and multiplied these measures to estimate expansion area. We calculated expansion rate by subtracting the expansion area recorded at each monitoring date by area measured at the previous monitoring date and dividing the difference by the number of days between sampling periods (cm<sup>2</sup> expansion/d). We also counted the total number of stems in each patch and calculated net stem production rate by calculating the difference in total stems recorded between sequential monitoring dates (density/d).

We analyzed the effect size and significance of disturbance type and patch size over time on patch lateral expansion and stem production rate metrics using a three-way disturbance type  $\times$  patch size  $\times$  time repeated-measures ANOVA. Similarly, final patch expansion area and stem count

were analyzed using a two-way disturbance type  $\times$  patch size ANOVA. For these ANOVA tests and other similar tests detailed below, any significant interactions were further investigated with separate ANOVA tests for each disturbance type and patch size, respectively, followed by post hoc comparisons using Tukey's HSD (Graham and Edwards 2001). To account for unequal sample size between sites and ensure that the  $P$ -values reported are a conservative estimate of significance, these data as well as those detailed below were analyzed with weighted means and type I sum of squares and were not corrected using the Satterthwaite approximation (Satterthwaite 1946). These analyses as well as all others that follow were analyzed in R using the *Agricolae* package (De Mendiburu 2014, R Core Team 2015).

After one year, we partitioned the space around each patch into four concentric quadrats (transplant, winter, spring, and summer) to capture potential differences among patch biomass of each size in each disturbance type in their pattern of lateral expansion over time. Square, rather than circular, seasonal expansion quadrats were used simply out of convenience. The transplant quadrat included the footprint of the initial circular transplant (10 cm diameter for small transplants, 25 cm diameter for medium/large transplants), "winter" from the boundary of the initial transplant to 15 cm from the patch center (0.05- or 0.08-m<sup>2</sup> footprint for small and medium/large initial core sizes, respectively), "spring" 15 cm beyond winter boundaries (a 0.27-m<sup>2</sup> footprint), and "summer" 60 cm beyond spring boundaries (a 1.1-m<sup>2</sup> footprint, see Appendix S1 for diagram). The expansion zones were established to represent the observed average lateral patch expansion during each season; we harvested a 1.4-m<sup>2</sup> area centered on each patch plot. Stems were clipped at ground level from each quadrat, washed, dried, and weighed. Dried aboveground biomass was calculated for each harvested patch (total of transplant, winter, spring, and summer quadrats).

To sample belowground biomass (BB), we extracted 4  $\times$  10 cm (diameter  $\times$  depth) cores at random points within each of the following locations: the initial transplant quadrat (one core/patch), and in winter and spring quadrats (three cores collected per quadrat/patch). BB was not measured in summer quadrats because cordgrass colonization

of this zone was highly spatially variable, limiting the reliability of BB estimates we could obtain from this sampling method. Cores were sorted into live root and rhizomes, dried, and weighed. We estimated total BB for each quadrat using the following equation: Total BB =  $(C_w/C_{SA}) \times A$ , where  $C_w$  is the sum of the dry weights of roots and rhizomes for the core sample(s),  $C_{SA}$  is the surface area of core(s), and  $A$  is the quadrat area. Quadrat area depended on quadrat type (transplant, winter, and spring) and initial transplant size (transplant [small and medium/large]: 78.5 and 491 cm<sup>2</sup>, respectively; winter [small and medium/large]: 821 and 409 cm<sup>2</sup>, respectively; and spring: 2700 cm<sup>2</sup>; Appendix S1). This allowed us to compare the total below- and aboveground biomass (total g dry plant material) for each quadrat harvested. Aboveground biomass and BB were analyzed using a three-way disturbance type  $\times$  patch size  $\times$  zone of harvest nested ANOVA, with zone of harvest nested within each patch.

#### *Abiotic and biotic factors*

To assess potential differences in soil organic matter (hereafter, SOM), a metric of residual root material in the soil that contributes to physical soil structure and may be affected differently by VD than by S + VD, between the two disturbance types in mudflat and reference areas near each disturbance mudflat, we collected five replicate soil cores from each nonvegetated mudflat plot and from vegetated reference areas at each site in September 2014 at the time of harvest ( $N = 20$ ), which we then subdivided into segments to represent stratigraphy of upper (0–5 cm) and lower (5–10 cm) rooting soil horizons. We oven-dried the soil samples at 65°C, ground them with mortar and pestle, sieved them through a 2-mm-mesh screen, and used the ash-free dry weight of 5 g subsamples of each sieved sample to determine the SOM proportion (see Craft et al. 1991 for details). To compare whether SOM differed in the vegetated (reference) marsh areas at the two sites, we tested the effect of site on SOM using Student's  $t$  tests; separate tests were conducted for shallow and deep soil core depths. The same Student's  $t$  tests were repeated to compare SOM between mudflat marsh areas at each depth at the two sites.

To characterize differences in chemistry of soil pore water that may be mediating cordgrass patch

growth, we measured reduction–oxidation potential, hereafter redox, a measure of soil oxygen availability, at 5 cm depth at three patch locations: the center of patches, 25 cm away from patch center in the area of vegetative expansion, and 40 cm away from patch center in bare soil taken during midday hours in July 2014 using a portable electrode (Orion Star probe and Accumet Portable ORP Meter, Thermo Fisher Scientific, Waltham, Massachusetts, USA). Redox potential was measured for 6 and 12 replicate patches of each size class at S + VD and VD, respectively. We also used rhizon samplers (Rhizosphere Research Products, Wageningen, The Netherlands) to extract pore water from the top 5 cm of soil at the same three patch locations as redox measurements. Pore water was extracted from four haphazardly chosen patches of each size class and from four reference plots at each site during low tide in July 2014. For each pore water sample, we measured ammonia concentration to assess plant available nitrogen, salinity to estimate drainage and evapoconcentration, and pH (Seal AQ2 Automated Discrete Analyzer AQ2 [Porvair Sciences, Norfolk, United Kingdom], Method EPA-104-A Rev. 4, Sentix 41 pH and Tetracon 325 conductivity probes [WTW, Weilheim, Germany]). Redox, ammonia, salinity, and pH response metrics were analyzed using three-way disturbance type  $\times$  patch size  $\times$  location within patch nested ANOVA with location nested within each patch.

In addition, we surveyed the relative abundance of periwinkle snails (*Littoraria irrorata*), fiddler crabs (*Uca pugnax* and *Uca pugilator*), and mud crabs (*Panopeus herbstii*). As snails can reduce cordgrass biomass (Silliman and Bertness 2002) and slow the expansion of remnant cordgrass patches (Angelini and Silliman 2012) via their grazing and farming of fungus on plant stems, we scored snail damage on five random cordgrass stems as the percentage of total leaf area wounded by snails and averaged these values for each patch. Because crab bioturbation can affect soil chemistry by creating conduits for air and water exchange (Bertness 1985, Gribsholt et al. 2003), we counted the number and measured diameter and depth of all crab burrows observed within a 65  $\times$  65 cm quadrat centered on each patch in both July and August 2014. From these measures, we estimated total volume (cm<sup>3</sup>; depth  $\times$  burrow surface area) of

burrows per unit area (m<sup>2</sup>) of marsh around each patch. Crab burrow volume was log-transformed to meet assumptions of normality and analyzed with a two-way disturbance type  $\times$  patch size ANOVA, while snail damage was analyzed using a three-way disturbance type  $\times$  patch size  $\times$  time repeated-measures ANOVA.

Finally, we used simple linear regression models to assess whether there exists a general relationship between crab burrow volume and anoxic stress (measured via redox potential) and between anoxic stress (again, via redox potential) and plant aboveground biomass. These analyses build off of prior studies that have demonstrated that fiddler crabs play a critical role in aerating otherwise anoxic marsh soils through their burrowing activities and, in doing so, stimulating grass production. Data from both disturbance types and all patch sizes were included in each analysis.

## RESULTS

### *Cordgrass patch expansion and performance*

Patch expansion across mudflats was dramatically higher in the VD compared with S + VD mudflat and also varied with patch size (site:  $F_{1,59} = 78.3$ ,  $P < 0.001$ ; patch size:  $F_{2,59} = 6.64$ ,  $P < 0.01$ ; Fig. 2a, b) despite both sites being exposed to a similar level of tidal inundation. Within the VD mudflat, large patches exhibited the greatest areal expansion, growing 12% larger than medium and 68% larger than small patches over one year (Fig. 2a). At the S + VD mudflat, in contrast, medium patches exhibited the greatest areal expansion, growing 46% more than large and 280% more than small patches (Fig. 2b). Expansion rates (cm<sup>2</sup>/d) differed between sites (site:  $F_{1,472} = 84.2$ ,  $P < 0.001$ ), but only VD exhibited differences between patch sizes and over time (patch size:  $F_{2,360} = 6.16$ ,  $P < 0.01$ , time:  $F_{8,360} = 24.4$ ,  $P < 0.001$ ; Fig. 2). In VD, patches of all size classes expanded at variable rates throughout the year with rates being highest from June to July ( $98.4 \pm 13.9$  cm<sup>2</sup>/d; Fig. 2a) and lowest from September to October ( $1.34 \pm 0.24$  cm<sup>2</sup>/d, Fig. 2a), while S + VD patches expanded at consistently low rates all year-long (maximum of  $9.19 \pm 4.93$  cm<sup>2</sup>/d). In VD, large patches expanded at the highest rate recorded over the year between June and July ( $144.1 \pm 22.1$  cm<sup>2</sup>/d; Fig. 2a), which was 25% faster than medium patches and 117%

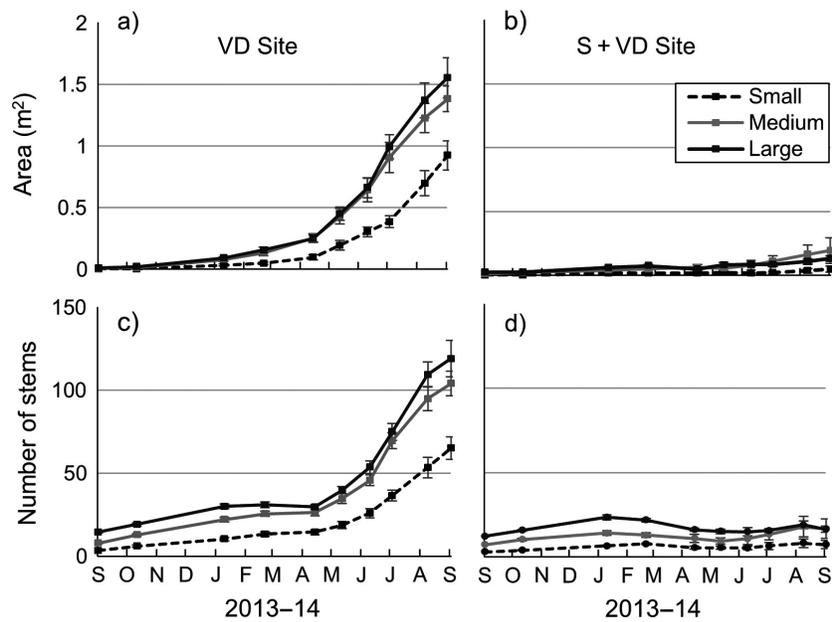


Fig. 2. Expansion area (a, b) and stem production (c, d) of small, medium, and large patches over 12 months in mudflats with vegetation-only (VD; left panels) and soil + vegetation disturbance (S + VD; right panels). Data are shown as the mean  $\pm$  SE of 16 and six replicate transplants of each size at the VD and S + VD mudflat sites, respectively.

faster than small patches. In contrast to continual, although temporally variable expansion of all patches at VD, the areal footprint of some patches in S + VD actually shrunk during some months (large patches:  $-4.8 \pm 4$  cm<sup>2</sup>/d in April,  $-1 \pm 3$  cm<sup>2</sup>/d in July, medium patches:  $-1.7 \pm 5$  cm<sup>2</sup>/d in May, and small patches:  $-0.2 \pm 1$  cm<sup>2</sup>/d in June,  $-1.2 \pm 3$  cm<sup>2</sup>/d in July, Fig. 2b).

Over the year-long experiment, large patch net stem production ( $118.9 \pm 11.0$  stems produced/yr) was 14% greater than medium and 83% greater than small patch net stem production in VD, rates that were 10 times higher than those recorded in S + VD (large and medium patches  $\sim 17$  and small patches  $\sim 8$  stems produced/yr, site:  $F_{1,59} = 91.7$ ,  $P < 0.001$ , patch size:  $F_{2,59} = 11$ ,  $P < 0.001$ , Fig. 2c, d). Stem production rate showed a similar trend to expansion rate, such that stem production rate differed between classes and over time in VD (patch size:  $F_{2,360} = 5.86$ ,  $P < 0.01$ ; time:  $F_{8,360} = 51.5$ ,  $P < 0.001$ ; Fig. 2c), but was consistently low regardless of patch size in S + VD with only slight net production over time (time:  $F_{8,112} = 2.86$ ,  $P < 0.01$ ; Fig. 2d). Between June and July, stem

production rates were highest in medium patches in both sites, but were an order of magnitude less in S + VD than in VD ( $1.0 \pm 0.09$  stems/d vs.  $0.11 \pm 0.04$  stems/d, respectively; Fig. 2c). Furthermore, while large and medium patch stem production rates began to slow in August and September in VD, small patch stem production rates remained unchanged throughout these early fall months. All patches in S + VD, in contrast, experienced some degree of stem loss in the early spring and early fall and only consistently produced additional stems and, thus, exhibited positive stem production rates in mid-summer (Fig. 2d).

Patterns in cordgrass biomass within VD and S + VD paralleled those for cordgrass expansion and stem production. Specifically, aboveground biomass was generally far greater in VD than in S + VD (site,  $F_{1,171} = 52.9$ ,  $P < 0.001$ ; Fig. 3). Aboveground biomass at both sites differed between zones of harvest within patches ( $F_{3,171} = 3.75$ ,  $P < 0.05$ ; Fig. 3), but only within VD were there marked differences in aboveground biomass between patch sizes (patch size:  $F_{2,129} = 5.35$ ,  $P < 0.01$ ; Fig. 3) and an interaction between

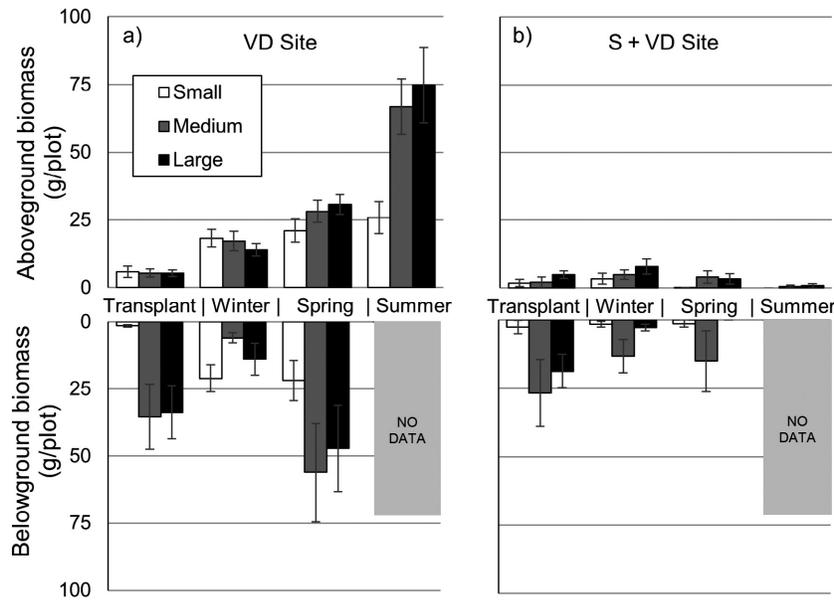


Fig. 3. The above- and belowground biomass (BB) of small, medium, and large transplants in vegetation-only (a) and soil + vegetation disturbance (b) mudflat sites. Values reflect actual total harvested aboveground biomass and estimates of total BB extrapolated from representative soil cores partitioned into initial transplant, winter expansion (transplant border  $-0.3$  m from center), spring expansion ( $>0.3-0.6$  m from center), and summer expansion ( $>0.6$  m from center) zones. Data are shown as the mean  $\pm$  standard error. Due to high spatial variability of BB in the “summer” expansion area, we did not extract cores from this zone.

zone of harvest and patch size (patch size  $\times$  zone of harvest:  $F_{6,129} = 5.6$ ,  $P < 0.001$ ) with the most biomass produced in large-sized patches in the summer expansion zone (Fig. 3a). Importantly, while we recorded the largest total aboveground biomass levels in the outermost summer expansion quadrat at VD, no cordgrass stems had colonized this quadrat in S + VD. Belowground, although root and rhizome biomass in large patches was similar to both small and medium patches, biomass was generally greater in medium compared

with small patches and, within VD, differed between spring and winter harvest zones (patch size:  $F_{2,106} = 4.44$ ,  $P < 0.05$ ; zone of harvest:  $F_{2,106} = 3.71$ ,  $P < 0.05$ ; Fig. 3).

#### Soil and community responses to disturbance

Soil cores indicated that SOM was similar in the reference marsh areas at both sites at both 0- to 5- and 5- to 10-cm horizons (Table 1). However, cores extracted from S + VD had significantly less SOM in the upper layer (0–5 cm) compared with

Table 1. Soil organic matter values (%) within mudflats of either vegetation disturbance (VD) or soil + VD (S + VD) compared with paired healthy reference marsh areas on Sapelo Island, Georgia, United States.

| Location of sample | Depth (cm)† | VD (mean $\pm$ SE) | S + VD (mean $\pm$ SE) | Residual d.f. | <i>P</i> -value (effect of disturbance type, <i>t</i> test) |
|--------------------|-------------|--------------------|------------------------|---------------|---|
| Mudflat            | 0–5         | 10.5 $\pm$ 0.5     | 6.5 $\pm$ 0.9          | 8             | <0.01**   |
| Vegetated marsh    | 0–5         | 8.4 $\pm$ 0.3      | 6.9 $\pm$ 0.5          | 8             | 0.99  |
| Mudflat            | 5–10        | 9.2 $\pm$ 0.4      | 6.3 $\pm$ 1.0          | 8             | 0.06  |
| Vegetated marsh    | 5–10        | 7.8 $\pm$ 0.4      | 7.3 $\pm$ 0.9          | 8             | 0.99  |

† Soil cores were divided into 5-cm increments to distinguish stratigraphy of upper (0–5) and lower (5–10) rooting horizons.

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

soil cores from VD ( $P < 0.01$ ; Table 1). Pore water chemistry analyses further revealed marked differences in patterns in ammonia concentrations and oxygen availability between sites. While ammonia levels were similar in reference marsh areas and between patch size classes within each site, they varied significantly between locations within patches (location:  $F_{3,54} = 34.4$ ,  $P < 0.001$ , Fig. 4), increasing with distance from the patch center. Ammonia concentrations were also four and three times higher in patch clonal expansion (25 cm from patch center) and bare mudflat (40 cm from patch center) locations, respectively, within patches at the S+VD compared with VD site ( $F_{1,54} = 40.7$ ,  $P < 0.001$ ; Fig. 4). Complementing

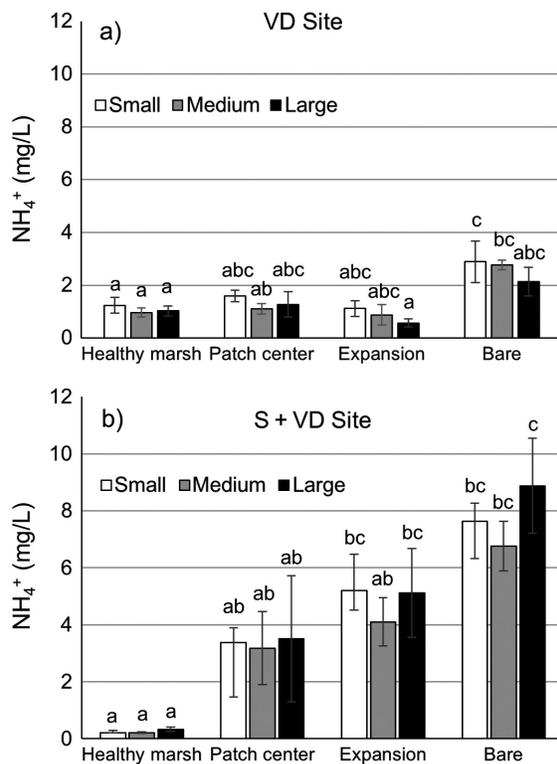


Fig. 4. Pore water ammonia concentrations in the top 5 cm of soil at vegetation-only (VD) and soil+vegetation disturbance (S+VD) mudflats and in reference marsh areas. Samples extracted within mudflat sites were located in the center of experimental transplants (core), 20 cm away from core (expansion), and in bare disturbance mudflat 40 cm from core (bare). Different shaded columns indicate different patch sizes, and different letters above columns indicate significant differences within VD and S+VD mudflats.

these data, redox potential was generally lower, indicating reduced oxygen availability in the bare mudflat at S+VD than at VD ( $-153 \pm 3$  mV vs.  $-5 \pm 15$  mV;  $F_{1,94} = 35.1$ ,  $P < 0.001$ ). Furthermore, although redox potential generally decreased with distance from patch center in S+VD ( $F_{2,30} = 8.01$ ,  $P < 0.01$ ; Fig. 5b), neither patch size nor location within patch drove a significant variation in this response variable within VD (Fig. 5a). Pore water salinity was slightly higher in S+VD compared with VD ( $F_{1,48} = 45.6$ ,  $P < 0.001$ ;  $34.4 \pm 0.42$  ppt vs.  $31.3 \pm 0.55$  ppt, respectively), while pH, although similar across sites, varied slightly between sample locations within patches (location:  $F_{3,48} = 6.9$ ,  $P < 0.001$ ; transplant center =  $7.05 \pm 0.05$ , transplant expansion =  $7.04 \pm 0.06$ , bare mudflat =  $7.19 \pm 0.05$ , vegetated reference =  $6.87 \pm 0.09$ ). However, these differences were not ecologically significant.

Crab burrow distribution and snail grazing intensity also differed between the two sites. Crab burrow volume was nearly five times greater in the VD than in the S+VD mudflat (site:  $F_{1,66} = 59$ ,  $P < 0.001$ ), but was similar across patch sizes within each site (Fig. 5c, d). The percentage of cordgrass leaves damaged by snails was overall greater in S+VD, compared to VD mudflat (site:  $F_{1,236} = 120$ ,  $P < 0.001$ ; Fig. 5e, f). Percentage leaf damage increased over time in the VD, but not in S+VD (VD, time:  $F_{4,180} = 35.7$ ,  $P < 0.001$ ), while leaf damage between patch sizes did not vary in the VD, but did in S+VD with larger patches having greater percentage leaf damage than smaller patches (S+VD, patch size:  $F_{2,45} = 5.06$ ,  $P < 0.05$ ).

#### Effects of soil and biotic factors on cordgrass performance

Regression analysis revealed a positive relationship between log-transformed crab burrow volume and redox potential in patches across both sites, indicating that increased burrowing crab activity partially explains the reduced anoxic stress (indicated by increased redox potential) we observed in the VD patches compared with S+VD patches ( $F_{1,47} = 10.6$ ,  $P < 0.01$ ,  $R^2 = 0.18$ ; Fig. 6a). Further, positive redox values were only recorded in the VD mudflats, while all values recorded in the S+VD were less than 140 mV and thus in the range of sulfate reduction. Also, we found a positive relationship between redox potential in each patch and

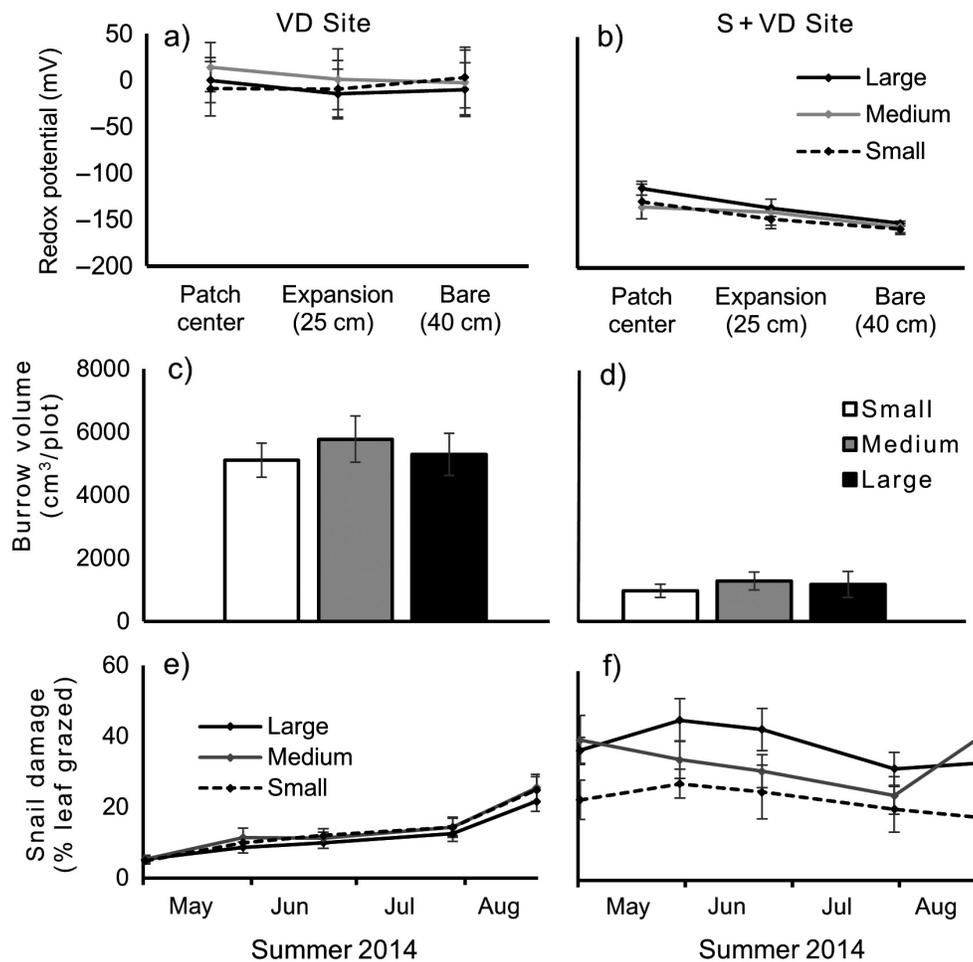


Fig. 5. Effects of disturbance type and cordgrass patch size on soil and plant characteristics including reduction–oxidation potential (a, b) in transplant patch center, 25 cm away from the center in the expansion area, and 40 cm away from center in the bare mudflat, crab burrow volume (c, d) measured within a 65 × 65 cm quadrat and snail grazing damage (e, f) on cordgrass transplant leaves monitored monthly from May to September 2014 in vegetation-only disturbance (VD; left panels) and soil + vegetation disturbance mudflat sites (S + VD; right panels).

cordgrass aboveground biomass ( $F_{1,47} = 13.9$ ,  $P < 0.001$ ,  $R^2 = 0.22$ ; Fig. 6b), suggesting that the lower anoxic stress observed in the VD patches partially explains increased plant biomass in those patches and thus crab burrowing may be indirectly stimulating plant biomass by creating local pockets of high oxygen availability.

## DISCUSSION

Collectively, these findings suggest that patch recolonization trajectories are far different after

disturbances that do not leave soil structure intact compared with those that do. While cordgrass performance and patch expansion are severely depressed in S + VD where soil is overturned and physically altered, remnant patches that are able to survive disturbances that leave soils structurally unaltered (VD) can expand rapidly across surrounding mudflats. These distinct recovery dynamics arise because of the different effects each disturbance type has on soil physical and chemical properties and associated faunal communities, with the intense physical soil

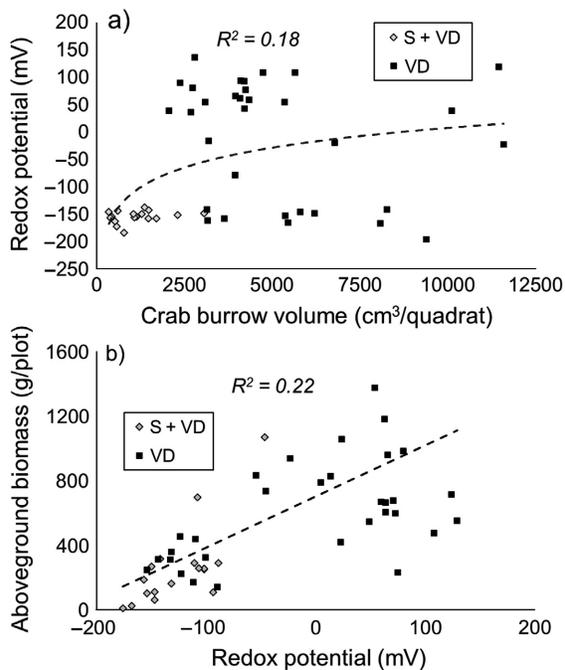


Fig. 6. Linear regression analysis of crab burrow volume and reduction–oxidation (redox) potential (a) and redox potential and aboveground plant biomass (b) in vegetation-only disturbance and soil + vegetation disturbance. Redox was measured at a depth of 5 cm near transplant cores, crab burrows were measured within a 65 × 65 cm quadrat, and aboveground biomass indicates total aboveground biomass harvested from plots one year after initial transplant. Analyses were performed across all sites and transplant plots.

disturbance associated with S+VD being prohibitive to cordgrass recovery. Vegetation-only disturbance caused by episodes of drought or wrack can likely recover to cordgrass dominance, especially where management efforts bolster the number and spatial distribution of remnant patches. We found that remnant patches of just 10–15 stems can revegetate approximately a square meter of mudflat and produce up to 180 stems within only 1 yr in VD mudflats, while equal-sized patches in S+VD mudflats struggle to maintain their original size and stem density. We suspect that each general disturbance type elicits similar effects on substrate structural integrity, soil biogeochemistry, and resident fauna in salt marshes across the southeastern U.S. region (S. Sharp and C. Angelini, *manuscript in prep*).

### Soil biogeochemistry across different disturbance types

The results from this study highlight mechanistic linkages among disturbance type, substrate characteristics, infauna, and the recovery of marsh vegetation. Some disturbances, while causing large-scale mortality of salt marsh vegetation, primarily remove the aboveground standing biomass and leave the underlying soil structure largely unaltered (Allison 1996, Tolley and Christian 1999, McKee et al. 2004). In contrast, disturbances that physically disrupt soil in addition to removing standing vegetation, like those caused by large herbivores, ecosystem engineers, or destructive land-use practices, not only remove standing plant biomass, but also turn marsh soils over and/or pound them into a slurry, leading to the surficial exposure and aeration of live and dead roots and rhizomes (Neill and Turner 1987, Ford and Grace 1998). In our soil analyses, we found that SOM, a measure influenced by the quantity of roots and rhizomes in the soil (Craft et al. 1999), was higher in the VD than in S+VD mudflats, despite these characteristics being similar in nearby healthy marsh areas at both sites (Table 1). We anticipate that enhanced aerial exposure of belowground plant material accelerates decomposition and loss of SOM in the overturned marsh soils that are characteristic of S+VD mudflats. Although the low SOM values measured in the hog-disturbed area may be partially explained by hog foraging on roots and rhizomes, these consumptive activities are more localized and sporadic than their more pervasive nonconsumptive activities (wallows and trampling), suggesting that oxidation of exposed SOM is the primary mechanism by which hogs drive SOM loss. A study on cultivation and tillage effects on pasture lands, a disturbance that leaves soil structure in a similar condition to hogs, found a 49% reduction in SOM in tilled compared with untilled pastures (Celik 2005). Combined, these findings indicate that soil-disrupting disturbances generally induce carbon mineralization. In addition to altering carbon cycling in salt marshes, SOM loss can also result in a drop in surface elevation, or marsh subsidence, as SOM contributes to maintaining soil volume (Day et al. 2011).

Through their initial impacts on SOM, we infer that differences in soil structural integrity in the VD and S+VD also influence the distribution and

burrowing ability of crabs, soil oxygen availability, and pore water chemistry (Figs. 4–6). While crabs can maintain deep, wide, structurally stable burrows in more rigid, root-dense soils, they struggle to do so in softer substrates where burrow walls easily collapse (Bertness et al. 2009). As crab bioturbation and burrowing aerate marsh soils to increase oxygen delivery, reduce toxic sulfide buildup in the plant rooting zone, and facilitate the flushing of stagnant pore water in VD (Bertness 1985, Gribsholt et al. 2003, Stahl et al. 2014), we correspondingly found that the loss of these activities in the S+VD was associated with reduced oxygen availability, a redox potential that corresponds to sulfate reduction and depressed plant growth (right panels Figs. 2, 4–6). Furthermore, in anoxic wetland soils, oxygen delivery plays a key role in modulating nitrification, a common soil microbial metabolic process that requires oxygen to transform ammonia ( $\text{NH}_4^+$ ) to nitrite ( $\text{NO}_2^-$ ). Where oxygen availability is relatively high, as in our VD mudflat site and control marsh areas, nitrification can proceed and ammonia levels remain relatively low, as indicated by our results (Figs. 4, 5b, d). In contrast, where oxygen levels are low, like in the S+VD, nitrification is arrested and ammonia can accumulate (Reddy et al. 1989), as we also observed. Disrupted soil from hog activity in a temperate deciduous forest similarly resulted in ammonia accumulation (Singer et al. 1984). From our results and these prior studies, we infer that bioturbation or soil disturbance can significantly alter biogeochemistry across a range of habitats. Interestingly, in salt marshes, the effects of soil disturbance on plant performance appear to shift from positive at small scales, such as those at which crab burrows aerate marsh soils around plant roots, to negative at larger scales, such as those at which hogs overturn swaths of marsh vegetation and soil and create environmental conditions prohibitive to plant growth (Mendelssohn and Postek 1982, Morris 1984).

#### *Patch growth, expansion, and associated feedbacks*

In the VD, we discovered that large and medium patches initially expand faster, produce more stems, and accrue more biomass than small patches. This supports part of our first hypothesis that, during the early months of the experiment, larger patches would grow and expand more than small patches. Although small patch

expansion area never converged with larger patches in the VD mudflat as predicted, their expansion rate eventually overtook that of large and medium patches after 11 months (Fig. 2a, c). This partially supported our second hypothesis that small patches would converge in size with larger patches over time. Overall, we found that cordgrass patch growth and expansion were exponential for all patch sizes in the VD site, suggesting that neither physical or biotic stressors in these mudflats nor initial patch size plays a critical role in plant recolonization of mudflats when soil remains physically unaltered (Fig. 2a, c). Others have found a similar relationship of rapid and widespread clonal expansion in environments with limited interspecific competition (review of aquatic plants: Santamaría 2002, Himalayan alpine tundra: Klimeš 2007). The robust growth we observed in this disturbance type seemed to be eventually modulated by increased resource competition; however, as we found that ammonia levels were increasingly depleted closer to medium and large patch centers (Fig. 4). Other studies of clonal plant growth in stressful environments found that intraspecific resource competition at high plant densities overshadowed facilitation benefits from conspecifics and limited the growth of larger plant aggregations (Maestre and Cortina 2004, Chu et al. 2008). More broadly, the fact that every transplanted patch expanded measurably over the year-long experiment highlights that any patch, regardless of its initial size or the strength of intraspecific competition it may experience, has the potential to contribute to marsh recovery in VD mudflats.

In the S+VD, patches recolonized only 1/10 the area that patches in VD recolonized, supporting our third hypothesis that growth and expansion of cordgrass patches across all size classes would be significantly less in this disturbance type. However, despite harsh abiotic conditions in S+VD and the potential benefits of stress amelioration provided by more conspecific neighbors, large patches did not continue to outpace small patch expansion as we predicted at this site (Fig. 2b). The elevated ammonia levels and visibly waterlogged soils suggest that anoxia, and an associated phytotoxin buildup, which has been shown to accumulate in “dieback” in other salt marsh systems (Goodman and Williams 1961), is the dominant factor controlling vegetative

regrowth of all patches, regardless of their size, in the S + VD (Figs. 2, 3, 5 right panels, 4b, 6). Anoxic soil has also been linked to reduced ammonia uptake in cordgrass (Morris 1984), a mechanism that may also contribute to the pooling of ammonia we observed in the S + VD. Additionally, snail damage was generally higher on cordgrass stems, although temporally variable, in the S + VD compared with VD (Fig. 5e, f). This may have been caused by the smaller numbers of stems per patch available to support the similar snail densities we observed across sites, or by cordgrass transplants being additionally stressed in the harsh, hog-disrupted mudflat making them more susceptible to snail grazing. In comparison, a study of a New England salt marsh recovery found lower herbivory and higher cordgrass patch survival in softer, muddy substrates (similar to those found in the S + VD disturbance), than in root-dense substrates (Altieri et al. 2013). In these marshes, root-dense, “peaty” substrate favored the system’s dominant crab herbivore, *Sesarma reticulatum*, which feed on live plant belowground tissue. Importantly, in southeastern U.S. marshes, we found that both physical and biotic stressors are enhanced in S + VD mudflats and are likely working together to prohibit marsh vegetation recovery from this widespread disturbance.

#### *Disturbance regimes, sea level rise, and the future of southeastern U.S. salt marshes*

Both disturbances that do and do not physically alter soil structure are increasing in frequency and duration globally as historic climate patterns are altered, human populations and resource consumption expand, and the introduction of adaptive and elusive problem species continue to plague our natural environments (Anthony et al. 2008, Estrada and Flory 2015, He and Silliman 2015). However, in this study we discovered that the environment created by physical soil disruption is prohibitive to the recovery necessary for disturbed marshes to shift from mudflat to cordgrass-dominated marsh states, whereas recovery after disturbances that only remove standing vegetation is rapid and can revegetate a mudflat in a single season. A return to a vegetated state is critical in maintaining the marsh building processes that regulate the ability of this system to keep pace with sea level rise (Morris et al. 2002). Additionally, disrupted soils

may further exacerbate marsh vulnerability to sea level rise by eliciting marsh subsidence through the loss of SOM, increasing the likelihood a marsh may convert to open water habitat (Singer et al. 1984, Ford and Grace 1998, Day et al. 2011). Impacts that physically alter soil structure in addition to removing standing vegetation, like those from hogs, nutria, or other ecosystem engineers in already stressed salt marshes of the southeast may be more impactful than previously thought, especially considering the persistent expansion of these animals and the potential for explosive population growth even after eradication measures have been taken (Ford and Grace 1998, Barrios-Garcia and Ballari 2012).

Understanding the nuances of different disturbances and their effects on ecosystem resilience, especially considering their potential to overlap in many places, can help inform disturbance-specific management strategies focused on protecting natural resources and valuable ecosystem services. Marsh management strategies that either preserve or plant an optimal distribution of remnant patches after disturbance where soil structure is left intact are likely to elicit rapid recovery of plants, associated communities, and ecosystem functions. In contrast, we recommend prioritizing proactive population control of problematic species like hogs, invasive nutria (*Myocastor coypus*), and *S. reticulatum*, to decrease their impacts on salt marshes, especially in locations where limited connectivity of these species to larger source populations may elevate the potential for successful eradication (Barrios-Garcia and Ballari 2012). Considering the variable effects of disturbance types and the interplay of local fauna on salt marsh recovery, we encourage that these differences be explored in other ecosystems and integrated into management and restoration efforts.

#### ACKNOWLEDGMENTS

We thank the Sapelo Island National Estuarine Research Reserve, Georgia Coastal Ecosystems LTER, University of Georgia Marine Institute, as well as the Kaplan, Brown, and Clark laboratories for the use of facilities and equipment. We also thank Caroline Reddy for assistance in the field and Jenet Dooley, Erica Hernandez, Lexie Liu Jing, Emily Persico, and Katherine Tran for help with field work. This research was supported by HT Odum Fellowship awarded to Sean Sharp and NSF-DEB 1546638 awarded to C. Angelini.

## LITERATURE CITED

- Alber, M., E. M. Swenson, S. C. Adamowicz, and I. A. Mendelssohn. 2008. Salt marsh dieback: an overview of recent events in the US. *Estuarine, Coastal and Shelf Science* 80:1–11.
- Allison, S. K. 1996. Recruitment and establishment of salt marsh plants following disturbance by flooding. *American Midland Naturalist* 136:232–247.
- Altieri, A., M. Bertness, and T. Coverdale. 2013. Feedbacks underlie the resilience of salt marshes and rapid reversal of consumer-driven die-off. *Ecology* 94:1647–1657.
- Angelini, C., J. N. Griffin, J. van de Koppel, L. P. M. Lamers, A. J. P. Smolders, M. Derksen-Hooijberg, T. van der Heide, and B. R. Silliman. 2016. A keystone mutualism underpins resilience of a coastal ecosystem to drought. *Nature Communications* 7:12473.
- Angelini, C., and B. R. Silliman. 2012. Patch size-dependent community recovery after massive disturbance. *Ecology* 93:101–110.
- Angelini, C., T. van der Heide, J. N. Griffin, J. P. Morton, M. Derksen-Hooijberg, L. P. M. Lamers, A. J. P. Smolders, and B. R. Silliman. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. *Proceedings of the Royal Society of London B: Biological Sciences* 282:20150421.
- Anthony, K. R. N., D. I. Kline, G. Diaz-Pulido, S. Dove, and O. Hoegh-Guldberg. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America* 105:17442–17446.
- Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81:169–193.
- Barrios-Garcia, M. N., and S. A. Ballari. 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biological Invasions* 14:2283–2300.
- Beck, M. W., et al. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51:633–641.
- Bertness, M. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology* 66:1042–1055.
- Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs* 57:129–147.
- Bertness, M., C. Holdredge, and A. Altieri. 2009. Substrate mediates consumer control of salt marsh cordgrass on Cape Cod, New England. *Ecology* 90:2108–2117.
- Bracke, M. B. M. 2011. Review of wallowing in pigs: description of the behaviour and its motivational basis. *Applied Animal Behaviour Science* 132:1–13.
- Cardoni, D. A., J. P. Isacch, M. E. Fanjul, M. Escapa, and O. O. Iribarne. 2011. Relationship between anthropogenic sewage discharge, marsh structure and bird assemblages in an SW Atlantic saltmarsh. *Marine Environmental Research* 71:122–130.
- Celik, I. 2005. Land-use effects on organic matter and physical properties of soil in a southern Mediterranean highland of Turkey. *Soil and Tillage Research* 83:270–277.
- Christie, M. C., K. R. Dyer, and P. Turner. 1999. Sediment flux and bed level measurements from a macro tidal mudflat. *Estuarine, Coastal and Shelf Science* 49:667–688.
- Chu, C. J., F. T. Maestre, S. Xiao, J. Weiner, Y. S. Wang, Z. H. Duan, and G. Wang. 2008. Balance between facilitation and resource competition determines biomass-density relationships in plant populations. *Ecology Letters* 11:1189–1197.
- Coverdale, T. C., C. P. Brisson, E. W. Young, S. F. Yin, J. P. Donnelly, and M. D. Bertness. 2014. Indirect human impacts reverse centuries of carbon sequestration and salt marsh accretion. *PLoS ONE* 9:1–7.
- Craft, C., J. Reader, J. N. Sacco, and S. W. Broome. 1999. Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecological Applications* 9:1405–1419.
- Craft, C. B., E. D. Seneca, and S. W. Broome. 1991. Loss on ignition and Kjeldahl digestion for estimating organic carbon and total nitrogen in estuarine marsh soils: calibration with dry combustion. *Estuaries* 14:175–179.
- Day, J. W., G. P. Kemp, D. J. Reed, D. R. Cahoon, R. M. Boumans, J. M. Suhayda, and R. Gambrell. 2011. Vegetation death and rapid loss of surface elevation in two contrasting Mississippi delta salt marshes: the role of sedimentation, autocompaction and sea-level rise. *Ecological Engineering* 37:229–240.
- De Leeuw, J., L. P. Apon, P. M. J. Herman, W. de Munck, and W. G. Beftink. 1992. Vegetation response to experimental and natural disturbance in two salt-marsh plant communities in the southwest Netherlands. *Netherlands Journal of Sea Research* 30:279–288.
- De Mendiburu, F. 2014. *Agricolae*: statistical procedures for agricultural research. R-package.
- Estrada, J. A., and S. L. Flory. 2015. Cogongrass (*Imperata cylindrica*) invasions in the US: mechanisms, impacts, and threats to biodiversity. *Global Ecology and Conservation* 3:1–10.

- Ford, M. A., and J. B. Grace. 1998. Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. *Journal of Ecology* 86:974–982.
- Goodman, P. J., and W. T. Williams. 1961. Investigations into “Die-back” in *Spartina townsendii* Agg.: III. Physiological correlates of “Die-back”. *Journal of Ecology* 49:391–398.
- Graham, M. H., and M. S. Edwards. 2001. Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. *Oikos* 93:505–513.
- Gribsholt, B., J. E. Kostka, and E. Kristensen. 2003. Impact of fiddler crabs and plant roots on sediment biogeochemistry in a Georgia saltmarsh. *Marine Ecology Progress Series* 259:237–251.
- Gustafsson, C., and C. Boström. 2013. Influence of neighboring plants on shading stress resistance and recovery of eelgrass, *Zostera marina* L. *PLoS ONE* 8:e64064.
- Halpern, C. B., P. M. Frenzen, J. E. Means, and J. F. Franklin. 1990. Plant succession in areas of scorched and blown-down forest after the 1980 eruption of Mount St. Helens, Washington. *Journal of Vegetation Science* 1:181–194.
- Hartman, J. M. 1988. Recolonization of small disturbance patches in a New England salt marsh. *American Journal of Botany* 75:1625–1631.
- He, Q., and B. R. Silliman. 2015. Biogeographic consequences of nutrient enrichment for plant-herbivore interactions in coastal wetlands. *Ecology Letters* 18:462–471.
- Herrero, J., S. Couto, C. Rosell, and P. Arias. 2004. Preliminary data on the diet of wild boar living in a Mediterranean coastal wetland. *Galemys* 16:115–123.
- Jefferies, R. L., A. P. Jano, and K. F. Abraham. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94:234–242.
- Johnson, E. A., and K. Miyanishi. 2007. Plant disturbance ecology: the process and the response. Academic Press, Cambridge, Massachusetts, USA.
- Klimeš, L. 2007. Clonal splitters and integrators in harsh environments of the Trans-Himalaya. *Evolutionary Ecology* 22:351–367.
- Maestre, F. T., and J. Cortina. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London B: Biological Sciences* 271:S331–S333.
- Mateos-Naranjo, E., S. Redondo-Gómez, C. J. Luque, E. M. Castellanos, A. J. Davy, and M. E. Figueroa. 2008. Environmental limitations on recruitment from seed in invasive *Spartina densiflora* on a southern European salt marsh. *Estuarine, Coastal and Shelf Science* 79:727–732.
- McKee, K. L., I. A. Mendelssohn, and M. D. Materne. 2004. Acute salt marsh dieback in the Mississippi River deltaic plain: A drought-induced phenomenon? *Global Ecology and Biogeography* 13:65–73.
- Mendelssohn, I. A., and M. T. Postek. 1982. Elemental analysis of deposits on the roots of *Spartina alterniflora* Loisel. *American Journal of Botany* 69:904–912.
- Morris, J. T. 1984. Effects of oxygen and salinity on ammonium uptake by *Spartina alterniflora* Loisel. and *Spartina patens* (Aiton) Muhl. *Journal of Experimental Marine Biology and Ecology* 78:87–98.
- Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83:2869–2877.
- Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* 28:167–177.
- Neill, C., and R. E. Turner. 1987. Backfilling canals to mitigate wetland dredging in Louisiana coastal marshes. *Environmental Management* 11:823–836.
- Odum, W. E., E. P. Odum, and H. T. Odum. 1995. Nature’s pulsing paradigm. *Estuaries* 18:547.
- Odum, E., and A. Smalley. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* 45:617–622.
- Pennings, S., et al. 2012. South Atlantic tidal wetlands. Pages 45–61 in A. Baldwin and D. Batzer, editors. *Wetland habitats of North America: ecology and conservation concerns*. University of California Press, Oakland, California, USA.
- Pennings, S. C., and M. D. Bertness. 1999. Using latitudinal variation to examine effects of climate on coastal salt marsh pattern and process. *Current Topics in Wetland Biogeochemistry* 3:100–111.
- Pennings, S. C., and R. M. Callaway. 2000. The advantages of clonal integration under different ecological conditions: a community-wide test. *Ecology* 81:709–716.
- Proffitt, C. E., S. E. Travis, and K. R. Edwards. 2003. Genotype and elevation influence *Spartina alterniflora* colonization and growth in a created salt marsh. *Ecological Applications* 13:180–192.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Reddy, K. R., W. H. Patrick, and C. W. Lindau. 1989. Nitrification-denitrification at the plant root-sediment interface in wetlands. *Limnology and Oceanography* 34:1004–1013.

- Santamaría, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica* 23:137–154.
- Satterthwaite, F. E. 1946. An approximate distribution of estimates of variance components. *Biometrics Bulletin* 2:110–114.
- Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the United States of America* 99:10500–10505.
- Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelssohn. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310:1803–1806.
- Singer, F. J., W. T. Swank, and E. E. C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. *Journal of Wildlife Management* 48:464–473.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239.
- Stahl, M. O., M. H. Tarek, D. C. J. Yeo, A. B. M. Badruzzaman, and C. F. Harvey. 2014. Crab burrows as conduits for groundwater-surface water exchange in Bangladesh. *Geophysical Research Letters* 41: 8342–8347.
- Tolley, P. M., and R. R. Christian. 1999. Effects of increased inundation and wrack deposition on a high salt marsh plant community. *Estuaries* 22: 944.
- Travis, S. E., and M. W. Hester. 2005. A space-for-time substitution reveals the long-term decline in genotypic diversity of a widespread salt marsh plant, *Spartina alterniflora*, over a span of 1500 years. *Journal of Ecology* 93:417–430.
- Voss, C. M., R. R. Christian, and J. T. Morris. 2013. Marsh macrophyte responses to inundation anticipate impacts of sea-level rise and indicate ongoing drowning of North Carolina marshes. *Marine Biology* 160:181–194.
- Wall, D. H., and R. A. Virginia. 1999. Controls on soil biodiversity: insights from extreme environments. *Applied Soil Ecology* 13:137–150.
- Wasson, K., and A. Woolfolk. 2011. Salt marsh-upland ecotones in central California: vulnerability to invasions and anthropogenic stressors. *Wetlands* 31:389–402.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45:229–299.
- Wood, G. W., and R. E. Brenneman. 1980. Feral hog movements and habitat use in coastal South Carolina. *Journal of Wildlife Management* 44:420–427.
- Zedler, J. B., and S. Kercher. 2005. Wetland resources: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30: 39–74.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1540/full>