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Response and Recovery of Low-Salinity Marsh Plant Communities to Presses and Pulses of Elevated Salinity

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Abstract

In estuaries, future variation in sea level and river discharge will lead to saline intrusion into low-salinity tidal marshes. To investigate the processes that control the differential response and recovery of tidal freshwater marsh plant communities to saline pulses, a 3 × 5 factorial greenhouse experiment was conducted to examine the effects of a range of salinity levels (3, 5, and 10 practical salinity units (PSU)) and pulse durations (5, 10, 15, 20, and 30 days per month) on community composition of tidal freshwater marsh vegetation. Recovery of perturbed communities was also examined after 10 months. The results showed that community composition was increasingly affected by the more-saline and longer-duration treatments. The increasing suppression of salt-sensitive species resulted in species reordering, decreased species richness, and decreased aboveground biomass. Most of the plant species were able to recover from low-salinity, short-duration saline pulses in less than 1 year. However, because not all species recovered in the heavily salinized treatments, species richness at the end of the recovery period remained low for treatments that were heavily salinized during the treatment period. In contrast, plant aboveground biomass fully recovered in the heavily salinized treatments. Although the magnitude and duration of pulsed environmental changes had strong effects on community composition, shifts in community composition prevented long-term reductions in productivity. Thus, in this study system, environmental change affected species composition more strongly than it did ecosystem processes.

Keywords Disturbance · Salinization · Freshwater marsh · Composition · Productivity

Introduction

Climate change and human activities are affecting natural systems in many ways, ranging from shifts in plant functional groups (Saintilan et al. 2014), to cascading effects through food webs (Winder and Schindler 2004), to changes in carbon and nutrient stocks (Neubauer 2013; Zhou et al. 2016). Ecologists are interested in forecasting the consequence of various environmental changes, so that predictions can improve management and conservation practices. Climate change manifests as both chronic (press) alterations in climate and resources and as an increasing frequency and intensity of extreme events or acute (pulse) alterations (Smith et al. 2009).

Ecological responses to acute alterations depend on the magnitude, duration, and timing of the disturbances and can range from individual mortality (Howard and Mendelssohn 1999b; Ma et al. 2015) to changes in community structure (Dieleman et al. 2015; Howard and Mendelssohn 2000; Thibault and Brown 2008) to changes in ecosystem function (Ciais et al. 2005). Pulsed disturbances may not cause permanent changes to an ecosystem, as post-disturbance recovery can bring the ecosystem back to its baseline conditions (Smith 2011). For example, Hoover et al. (2014) imposed an extreme drought and heat wave in a grassland and found that aboveground net primary productivity recovered completely the year after the drought. When considering disturbances and ecological responses, researchers tend to focus primarily on pure press or pulse designs. However, natural disturbances often involve complex changes in magnitude, duration, and frequency over time (Donohue et al. 2016). This complexity indicates that restricting our focus to a single type of

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disturbance may cause us to misunderstand the impacts of abiotic change on community and ecosystem processes.

Coastal wetlands provide valuable ecosystem services to human society, including wildlife habitat, carbon sequestration, water quality improvements, and denitrification (Costanza et al. 1998; Zedler and Kercher 2005). The vegetation species diversity and composition of tidal marshes (freshwater, brackish, and salt marshes) along an estuary are determined by salinity (from freshwater to euryhaline) interacting with competition (Crain et al. 2004, Guo and Pennings 2012, Guo et al. 2014). Therefore, coastal wetland ecosystems are sensitive to climatic and anthropogenic changes that affect salinity, such as sea level rise, changed precipitation patterns, and reduced freshwater inflow due to human activities (Barendregt and Swarth 2013; Cloern and Jassby 2012; Knighton et al. 1991; Sklar and Browder 1998; Wood and Harrington 2015). Low-salinity marshes support higher primary productivity and total carbon and nitrogen stocks than salt marshes (Więski et al. 2010). Moreover, productivity of a dominant plant in many of these marshes, *Zizaniopsis miliacea*, varies from year to year as a function of freshwater discharge from rivers (Li et al. 2018). Therefore, salinization of these habitats caused by sea level rise, drought, or freshwater withdrawal from rivers could affect both plant productivity and composition (Neubauer 2013; Sutter et al. 2015).

A number of experimental studies have contrasted a constant low versus a constant elevated salinity treatment to test the effects of saline intrusion, showing that prolonged saline presses cause mortality of salt-sensitive species and shift wetland communities towards species with greater salinity tolerance (Pezeshki et al. 1987; Sharpe and Baldwin 2012; Woo and Takekawa 2012). Freshwater plants may be resilient to short-term saline pulses, however, and be able to recover once the pulses are withdrawn (Flynn et al. 1995; Hopfensperger et al. 2014). Howard and Mendelssohn (1999b) found that oligohaline marsh macrophytes in Louisiana, USA varied in their ability to recover from saline pulses. They found that *Schoenoplectus pungens* (referred to as *Scirpus americanus* by Howard and Mendelssohn) was able to fully recover from even the most extreme experimental conditions of exposure to 12 g/L salinity for 3 months, while the recovery of three other species (*Eleocharis palustris*, *Panicum hemitomon*, and *Sagittaria lancifolia*) decreased with increased salinity and increased duration. If saline pulses change community composition, this is likely to change how the wetlands function (Tilman et al. 1997; Hooper and Vitousek 1997; Spaak et al. 2017). Given long-term projections of sea level rise, locations currently dominated by tidal freshwater marshes are expected to transition to brackish or salt marshes as plant communities migrate upstream (Craft et al. 2009). One of the consequences of salinity pulses in tidal fresh wetlands is likely to be the release of nutrients from soils, either by cation exchange, desorption, or increased decomposition (Weston et al. 2006; Ardón et al. 2013; Dijk et al. 2015), and this may partially mediate the effects of increased salinities by providing plants with more nutrients. Conceivably, a plant in a low-salinity marsh that was a poor competitor but tolerant of moderate salinities could even benefit from salinization due to the decreased biomass of competitors and the increase in available nutrients. Given the complexity of the pulse events and differences among species in the affected communities, the ecological impacts of pulses of saline intrusion into low-salinity marshes are difficult to predict.

To investigate the processes that control the differential response and recovery of tidal freshwater marsh plant communities to saline pulses, we exposed mesocosms in Georgia, USA to saline water pulses consisting of three salinities for five durations and assessed both the immediate effects on the plant communities and their subsequent recovery in the absence of salinity stress. We tested the null hypothesis that saline water addition had no impacts on plant community composition and production. We expected this hypothesis to be rejected and predicted that increases in length of time exposed to salinity would result in community shifts towards more salt-tolerant species and reduced plant production but that the community composition and biomass would recover once the saline intrusion stopped.

Materials and Methods

We established mesocosm communities using six common freshwater plant species (*Z. miliacea*, *Pontederia cordata*, *Persicaria hydropiperoides* (=*Polygonum hydropiperoides*), *Peltandra virginica*, *Ludwigia repens*, *S. lancifolia*, and *E. palustris*) that together represent > 75% of the biomass of tidal freshwater plant communities along the Altamaha River estuary, Georgia, USA (authors' personal observations; common names given in Online resource 1). We collected all plants in a single tidal freshwater marsh (31° 20′ 16″ N, 81° 27′ 52 ″ W) between April 19 and 22, 2014. We collected sediment for the mesocosms from a freshwater pond (31° 23′ 54 ″ N, 81° 16′ 47″ W) on Sapelo Island, GA. The experimental mesocosms consisted of plastic round pools (height = 18 cm, diameter = 122 cm) filled to ~ 5 cm from the top with homogenized sediment. We planted each mesocosm with two individuals each of *Z. miliacea*, *P. cordata*, *P. virginica*, and *S. lancifolia* and five to eight individuals of *P. hydropiperoides* and *L. repens*. *E. palustris* was present in the root balls of the other species and so was not planted separately. For each species, we collected individual culms at least 5 m apart to minimize the chance that they were genetically identical. Mesocosms were located outdoors in a field 70 m from a natural salt marsh that was ~ 20 km downstream from the collection site and were therefore exposed to ambient temperature, humidity, and light regimes. After planting, mesocosms were watered with freshwater for 30 days until the experiment began.

From May 22 to August 19, 2014, we watered the mesocosms with three salinity levels (3, 5, and 10 PSU) crossed with five exposure durations (5, 10, 15, 20, and 30 days per month), plus a freshwater control treatment, for 16 treatment combinations ($n = 3$ per treatment combination). Except for the 30-day exposure treatment, which was a permanent saline press, mesocosms received freshwater in between pulses of saline water. For example, the 5-day treatment was watered with saline water for 5 days followed by freshwater for 25 days, and then the cycle was repeated. Different salinities were achieved by mixing tap water with seawater. We restricted the salinity range from 0 to 10 PSU because that is the range of salinities commonly observed in the freshwater marsh in the Altamaha River, GA, where the plants were collected (Li and Pennings 2018). We simulated tidal variation during the treatment period by watering the plants every morning and then pumping out water through a 6-in. (15 cm) slotted well (constructed of PVC pipe) every afternoon. Thus, this approach mimicked flooding of the marsh with water of different salinity levels. Porewater salinities no doubt did not respond instantly to changes in the salinity of flood water, and the response of the porewater was probably a complicated function of depth and proximity to the well. For logistical reasons, we did not monitor this daily, but we did measure porewater salinity on two dates. We inserted rhizon samplers (Eijkelkamp, Giesbeek, Netherlands) into soils to a depth of 5–10 cm to collect in situ porewater samples on two dates during the treatment period (July 20, 2014 and August 10, 2014) in order to measure effects of the treatments on porewater salinity and nutrient levels. Salinity was measured with a refractometer. Because porewater salinities were sampled on only two dates, without reference to any particular point in the salt-fresh cycle of each treatment, they do not reflect the dynamics caused by the salt-fresh cycle, and we do not analyze the data formally. Nevertheless, the salinity data show that porewater salinities generally increased with the duration and salinity treatments (Online resource 2). Control mesocosms had measured salinities of zero. Mesocosms watered with 3 PSU water had salinities ranging from 0 to 5, mesocosms watered with 5 PSU water had salinities ranging from 0 to 7, and mesocosms watered with 10 PSU water had salinities ranging from 0 to 15. For each salinity level, porewater salinities increased with the duration of the salinity treatment. We sent the water samples to the Stable Isotope Ecology Laboratory at the University of Georgia for total ammonium and phosphate content analysis. We did not measure nitrate content because previous work indicated that nitrogen would be present mostly as ammonium (Herbert et al. 2018).

From August 20, 2014 to June 30, 2015, we watered all mesocosm communities with freshwater to follow recovery. We did not simulate tidal variation during the recovery period. Instead, we watered all treatments twice a week to maintain the water level at least 3 cm above the sediment.

We measured the percent cover of all species present, and recorded species richness within each mesocosm, at the end of the treatment (August 12, 2014) and recovery (June 30, 2015) periods. At the end of the recovery period, we also measured the height of all *Z. miliacea*, *P. cordata*, *P. virginica, S. lancifolia*, and *P. hydropiperoides* plants. We then harvested the aboveground biomass of plants in each mesocosm (July 3 to July 31, 2015). We sorted plants to species, washed them to remove soil, and dried them at 60 °C to constant mass. Using the post-recovery data, we created allometric relationships between biomass and plant height (the sum of all plant heights for the species in one mesocosm; $n = 48$) or cover ($n = 48$) for all species and then used these relationships to estimate aboveground biomass during the treatment period (Online resource 1).

To examine the compositional dissimilarity of plant communities across the plots, we used nonmetric multidimensional scaling (NMDS) and compared dissimilarities using permutational multivariate analysis of variance (PERMANOVA). Both analyses were performed based on Bray-Curtis dissimilarity using the software package PAST ver. 3.11. The algorithm implemented in PAST was based on a new approach developed by Taguchi and Oono (2005). To describe internal community temporal dynamics, we used rank-abundance curves based on species biomass (Collins et al. 2008). To examine the treatment effects and the relationship between species richness and aboveground biomass, we conducted multiple linear regression analysis for species richness and biomass at the end of the treatment and recovery periods, with salinity, duration, and their interactions with richness or biomass as predictor variables. We also used multiple linear regression analysis to examine the effects of salinity, duration, biomass, and their interactions on porewater ammonium and phosphate content during the treatment period. Regression analyses were conducted with JMP 10.0 statistical software (SAS Institute Inc.). Data from this study are available on the GCE-LTER data portal (Li 2017).

Results

With increasing salinity levels and increasing salinity exposure duration, the plant community composition diverged from the control treatment (Fig. 1, PERMANOVA, salinity, $p < 0.01$; duration, $p < 0.01$; interaction, $p = 0.98$). The divergence of community composition was due to shifts in relative abundance of the species and species extinctions (Online resource 3). *E. palustris* was nearly always the highest-ranked species in all treatments, suggesting that it was robust to saline pulses. *S. lancifolia* and *Z. miliacea* were also relatively resistant to the saline treatments and maintained their biomass in most of the mesocosms. In contrast, *L. repens*

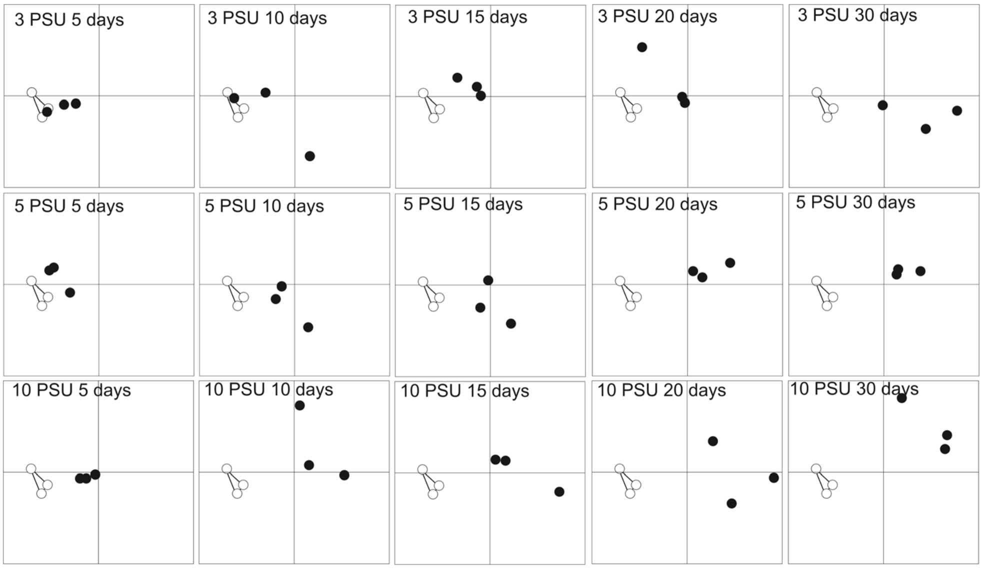

Fig. 1 Nonmetric multidimensional scaling (NMDS) plots showing the plant community composition of all plots in two-dimensional ordination space at the end of the treatments (August 12, 2014). Data are shown in 15 panels for clarity, with the control treatment shown in each. Each symbol represents the community composition based on aboveground biomass of all the species in a single plot. Control plots (open circles joined with lines) are the same in every plot; filled circles represent each treatment combination. 2D Stress = 0.12

and *P. hydropiperoides* were strongly suppressed by the more extreme saline treatments. *L. repens* was most abundant in the control treatment but eventually disappeared in mesocosms treated with 3 PSU water for 20 or 30 days, 5 PSU water for more than 5 days, and 10 PSU water for any duration. Similarly, *P. hydropiperoides* disappeared in mesocosms exposed to 5 PSU water for 30 days or 10 PSU water for more than 5 days. The rank abundance of *P. cordata* also dropped in mesocosms exposed to the highest salinity treatments (5 PSU water for 20 and 30 days and 10 PSU water for more than 5 days). *P. virginica* established poorly was the least abundant species in almost all mesocosms, and its responses are therefore difficult to interpret. It survived in all the 3 PSU treatments but in only half of the treatments with 5 and 10 PSU water. At those salinity ranges, however, it was present in some of the most severe treatments (5 PSU for 20 days, 10 PSU for 30 days) while disappearing in some of the less severe treatments (5 PSU for 15 days, 10 PSU for 10 and 15 days).

At the end of the treatment period, species richness declined with increasing salinity after 8 days of exposure (Fig. 2 and Table 1). Total aboveground biomass was negatively related to duration with salinity of 3 and 10 PSU and was strongly reduced in 10 PSU treatments compared to other salinities with same duration (Fig. 2 and Table 1). Salinity, duration, and their interaction explained 76% of the variability in species richness (Table 1, simple model). By adding biomass and interactions between the predictor variables, we explained slightly more of the variability in the data set (Table 1, complex model). Aboveground biomass at the end of the treatment period was negatively related to both salinity and duration but not their interaction (Table 1).

Ammonium concentration in porewater in July was positively related to salinity, duration, and the interaction of salinity and plant biomass (Fig. 3a and Table 2). A similar pattern persisted into August, but the concentration of ammonium was lower (Fig. 3b) and was affected not only by salinity, pulse duration, and their interaction but also by the interaction between pulse duration and plant biomass and their three-way interaction (Table 2). The concentration of phosphate in porewater was slightly higher in plots that were treated with high-salinity water and like ammonium decreased in all plots in August (Fig. 3). In July, the phosphate content was affected positively by salinity and negatively by pulse duration and plant biomass, while in August, it was affected by salinity and the interaction between pulse duration and plant biomass (Table 2).

After the 10-month recovery period, mesocosms did not converge on each other or on the control treatment but instead continued to diverge (Fig. 4). Different salinization patterns determined the trajectory of the mesocosms relative to the control treatment. Mesocosms that were treated with 3 PSU water for 5 and 10 days and 5 PSU water for 5 days followed the same general trajectory as the control mesocosms (Fig. 4a). With increasing treatment salinity and exposure duration, mesocosms increasingly diverged away from the controls and from each other (Fig. 4b, c). Overall, during the recovery period, the dissimilarity between the treatment mesocosms and the controls increased with both salinity (PERMANOVA, $p < 0.01$) and duration ($p < 0.01$) but not their interaction ($p = 0.94$).

The community composition of the mesocosms at the end of the treatment period and the end of the recovery period did not overlap in ordination space (Fig. 4). This was largely due to five species (*Cyperus odoratus*, *Lilaeopsis chinensis*, *Juncus marginatus*, *Schoenoplectus tabernaemontani*, and *Typha latifolia*) that emerged in all the plots as volunteers (not deliberately planted) during the recovery period

(Online resource 4). The reason that low salinization mesocosms (3 PSU for 3 and 10 days, 5 PSU for 5 days) recovered along the same general trajectory as the controls was that *L. repens* reappeared in these mesocosms. After the recovery period, *L. repens* biomass in mesocosms that were treated with 3 PSU water, 5 PSU water for 5 and 10 days, and 10 PSU water for 5 days was similar or greater than in the controls (Online resource 4). In contrast, *L. repens* remained absent in plots treated with 3 PSU for 20 and 30 days, 5 PSU water for 30 days, or 10 PSU water for more than 5 days. *E. palustris* was the highest-ranked species in all mesocosms. *P. hydropiperoides* recovered to levels similar to the control treatment in all mesocosms. *P. cordata* ended up with similar or even higher biomass in mesocosms that were treated with 3 PSU water, 5 PSU water for less than 30 days, and 10 PSU water for 5, 10, and 15 days compared to the controls.

At the end of the recovery period, plant species richness was negatively related to treatment salinity and duration but not their interaction (Fig. 5a and Table 1). These patterns persisted because the most salt-sensitive species, *L. repens*, which disappeared during the treatment period did not reappear in the previously more-saline treatments during the recovery period (Online resource 4). Aboveground biomass in the mesocosms was no longer related to salinity and increased slightly in mesocosms that had received a longer salinity exposure during the treatment period; however, this relationship explained less than 10% of the variation in final biomass (Fig. 5b and Table 1).

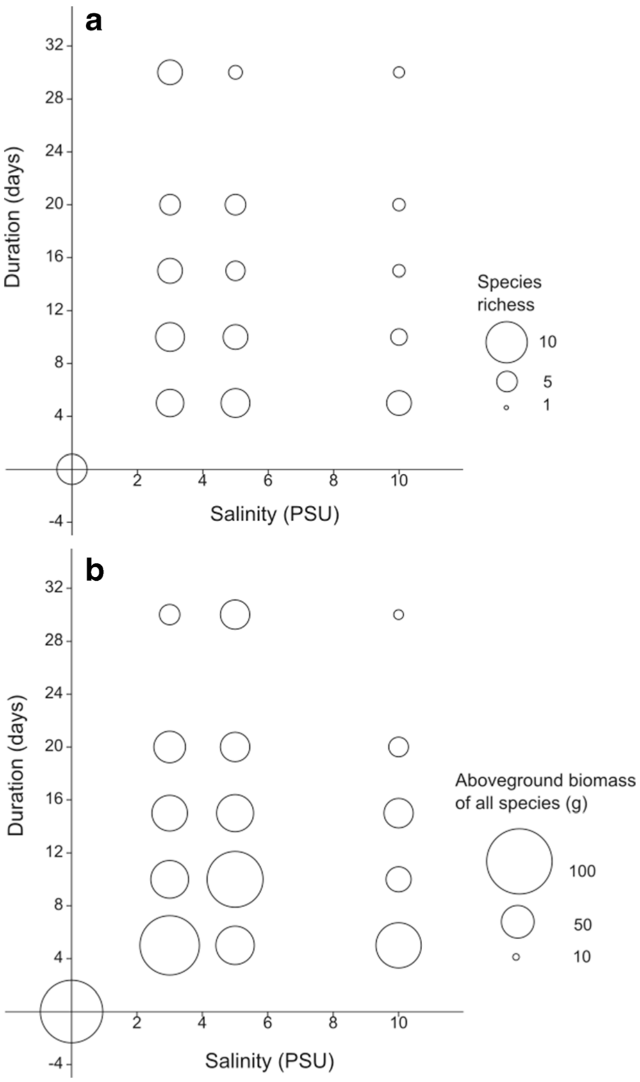

Fig. 2 Effects of exposure duration and salinity level on **a** species richness and **b** aboveground biomass of all species at the end of the treatment period (August 12, 2014)

Discussion

Salinization of coastal wetlands can occur on many time scales, from a gradual and prolonged change due to the long-term trend of sea level rise (Knighton et al. 1991; Wood and Harrington 2015) to acute and periodic pulses due to drought (Goodman et al. 2010; Visser et al. 2002;

Table 1 Best multiple linear regression models for species richness and biomass at the end of the treatment period and the end of the recovery period

		R^2	P
Species richness			
End of treatment (simple model)	Species richness = 8.39 − 0.31 S* − 0.09 D* − 0.001 (S − 5.62) × (D − 15)*	0.76	< 0.01
End of treatment (complex model)	Species richness = 9.57 − 0.38 S* − 0.13 D* − 0.01 B − 0.02 (S − 5.62) × (D − 15)* − 0.002 (D − 15) × (B − 54.14)* − 0.0002 (S − 5.62) × (D − 15) × (B − 54.14)*	0.83	< 0.01
End of recovery	Species richness = 9.27 − 0.19 S* − 0.08 D*	0.39	< 0.01
Biomass			
End of treatment	Biomass = 94.98 − 2.70 S* − 1.71 D*	0.47	< 0.01
End of recovery	Biomass = 138.38 + 1.52 D*	0.09	0.04

Predictor variables examined were salinity (S), duration (D), biomass (B, for species richness), and their interactions; the best model was selected based on Mallow's Cp statistic. For end of treatment species richness, the best model was quite complex, so we also report a simpler model that performed almost as well. Asterisks indicate significance (< 0.05) of individual term in the model

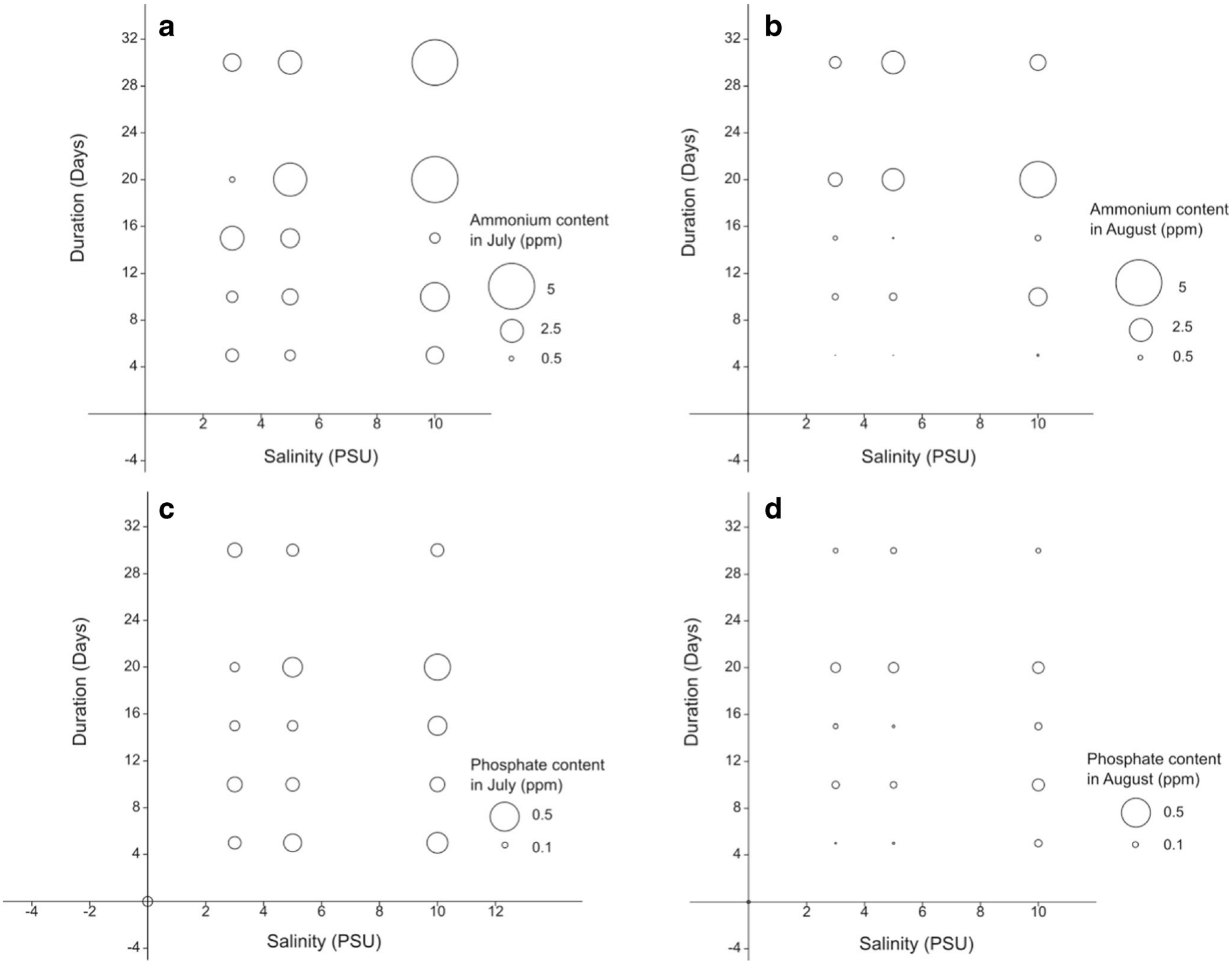

Fig. 3 Effects of exposure duration and salinity level on porewater ammonium concentration in **a** July and **b** August and phosphate concentration in **c** July and **d** August 2014

White and Alber 2009). Although freshwater marshes are projected to be replaced by brackish or salt marshes given prolonged salinization (Craft et al. 2009), marsh plant communities can recover from short-term saline pulses (Flynn et al. 1995; Hopfensperger et al. 2014; Howard and Mendelssohn 2000). Our results supported the hypothesis that the responses and recovery of tidal marsh vegetation were directly related to the salinity and duration of saline pulses. Higher-salinity, longer-duration saline pulses caused community composition shifts towards more salt-tolerant species, as

Table 2 Best multiple linear regression model for porewater ammonium and phosphate content in July and August, 2014

		R^2	P
Ammonium			
July 2014	Ammonium = $0.23\ S^* + 0.08\ D^* - 0.62\ (S - 5.62) \times (B - 1.58)^* - 0.44$	0.37	< 0.01
August 2014	Ammonium = $0.21\ S^* + 0.10\ D^* + 0.02\ (S - 5.62) \times (D - 15)^* + 0.19\ (D - 15) \times (B - 1.66)^* + 0.04\ (S - 5.62) \times (D - 15) \times (B - 1.66)^* - 1.37$	0.40	< 0.01
Phosphate			
July 2014	Phosphate = $0.01\ S^* - 0.005\ D - 0.19\ B^* + 0.55$	0.25	< 0.01
August 2014	Phosphate = $0.01\ S + 0.01\ (D - 15) \times (B - 1.66) + 0.08$	0.14	0.04

Predictor variables examined were salinity (S), duration (D), and plant biomass (B); the best model was selected based on Mallow's Cp statistic. Biomass was the sum of all species biomasses estimated using measurements of plant height and cover measured on July 14, 2014 or August 1, 2015 as appropriate and was log-transformed to improve normality. Asterisks indicate significance (< 0.05) of individual term in the model

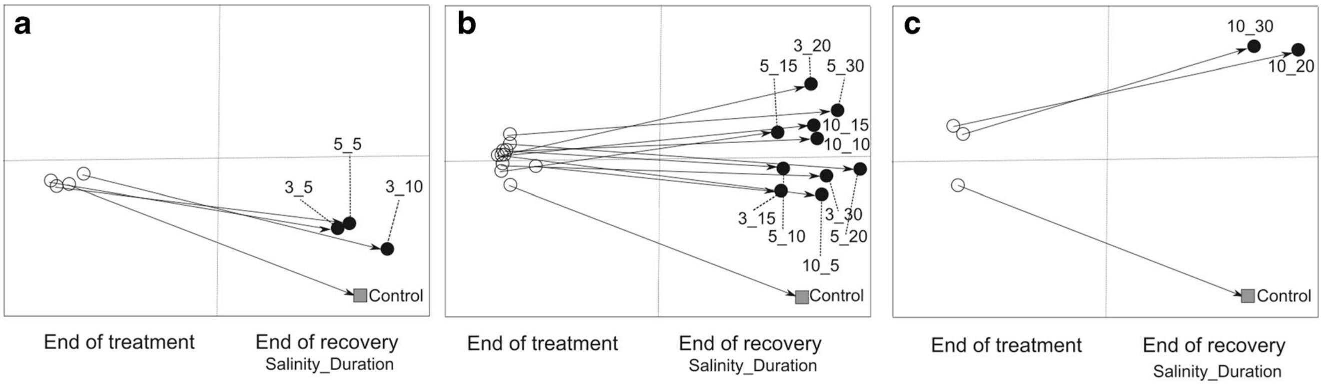

Fig. 4 Nonmetric multidimensional scaling (NMDS) plots showing recovery patterns of all plots in two-dimensional ordination space. Data are shown in three panels for clarity, with the control treatment shown in all three panels. The division of the data into the three panels was done subjectively to improve clarity, could have been done using other groupings, and does not imply statistical differences among the particular groups of treatments. Open and filled symbols represent the end-of-treatment (August 12, 2014) and end-of-recovery (June 30, 2015) community compositions based on aboveground biomass. Each point is coded as "salinity_duration." 2D Stress = 0.11

well as towards lower species richness and lower aboveground biomass, as measured immediately after the treatment period of the experiment. However, results differed after the communities were allowed to recover from saline exposure for ~ 10 months. Communities experiencing low-salinity and short-duration saline pulses recovered due to the regrowth of salt-sensitive species. Community composition of heavily salinized treatments did not recover, but aboveground biomass did, indicating that ecosystem processes may be more resilient to saline pulses than community composition. However, the caveat to this result is that our allometric relationships for *P. virginica*, *S. lancifolia*, and *E. palustris* did not have particularly high R^2 values, so we have a poor estimate of biomass of these species during the treatment period.

The salinity treatments affected all the plant species, but the magnitude of the effect varied with species. *L. repens* was the most salt-sensitive species, followed by *P. hydropiperoides*. Somewhat more resistant to salinity were *P. cordata*, which disappeared in mesocosms with 10 PSU water for more than 10 days, and *Z. miliacea*, which was present in all mesocosms. These results were consistent with a previous greenhouse experiment in which plant monocultures, lacking interspecific competition, in small (12 L) pots were exposed to multiple salinity treatments. In that experiment, Li and Pennings (2018) found that *Z. miliacea* was more robust to low-salinity pulses than *P. hydropiperoides* or *P. cordata*. The most resistant species in the mesocosms were *S. lancifolia* and *E. palustris*, which maintained similar abundances in control and saline mesocosms, except that they were both suppressed by continual watering with 10 PSU water. Unlike Howard and Mendelssohn (1999a), who found that *S. lancifolia* was affected earlier and for a longer extent by saline water addition than *E. palustris*, we found little difference between these two species in tolerance to saline pulses in our study. *P. virginica* established poorly in almost all mesocosms (perhaps the soil was too shallow for it to root effectively), and its responses are therefore difficult to interpret. It survived in all the 3 PSU treatments but at higher salinities disappeared in some of the less stressful treatments while surviving in some of the more stressful treatments. The simplest interpretation of this pattern is that it was haphazard given the very low abundance of *P. virginica* across all replicates. An alternative interpretation, which would take more work to confirm, is that *P. virginica* benefitted from the reduced plant biomass and species richness in the saltier treatments, which presumably led to less competition.

Based on the responses in this study, we ranked the species as follows, in order from least to most salt-tolerant: *L. repens* (because it disappeared in all nearly all treated plots without recovery in plots treated with 3 PSU for 20 and 30 days, 5 PSU water for 30 days, or 10 PSU water for more than 5 days), *P. hydropiperoides* (because it disappeared in plots treated with 5 PSU water for 30 days and 10 PSU water for more than 5 days but recovered in all mesocosms), *P. cordata* (because it disappeared in plots treated with 5 PSU water for 30 days and 10 PSU water for more than 5 days but recovered in all mesocosms), and *Z. miliacea* (because it survived in all treatments, but its abundance was lower than *S. lancifolia* and *E. palustris*), followed by *S. lancifolia* and *E. palustris* in a tie (because these two species persisted in all the treatments with high abundance).

Due to different salinity tolerances of the studied species, community composition was increasingly affected by the more-saline and longer-duration treatments. The increasing suppression of salt-sensitive species resulted in species reordering, decreased species richness, and decreased aboveground biomass. This pattern is observed in nature where plant species richness and productivity are typically higher in tidal freshwater marshes than in salt marshes (Odum 1988; Więski et al. 2010).

Although salinization was directly stressful to the plants that we studied, this effect may have been partially

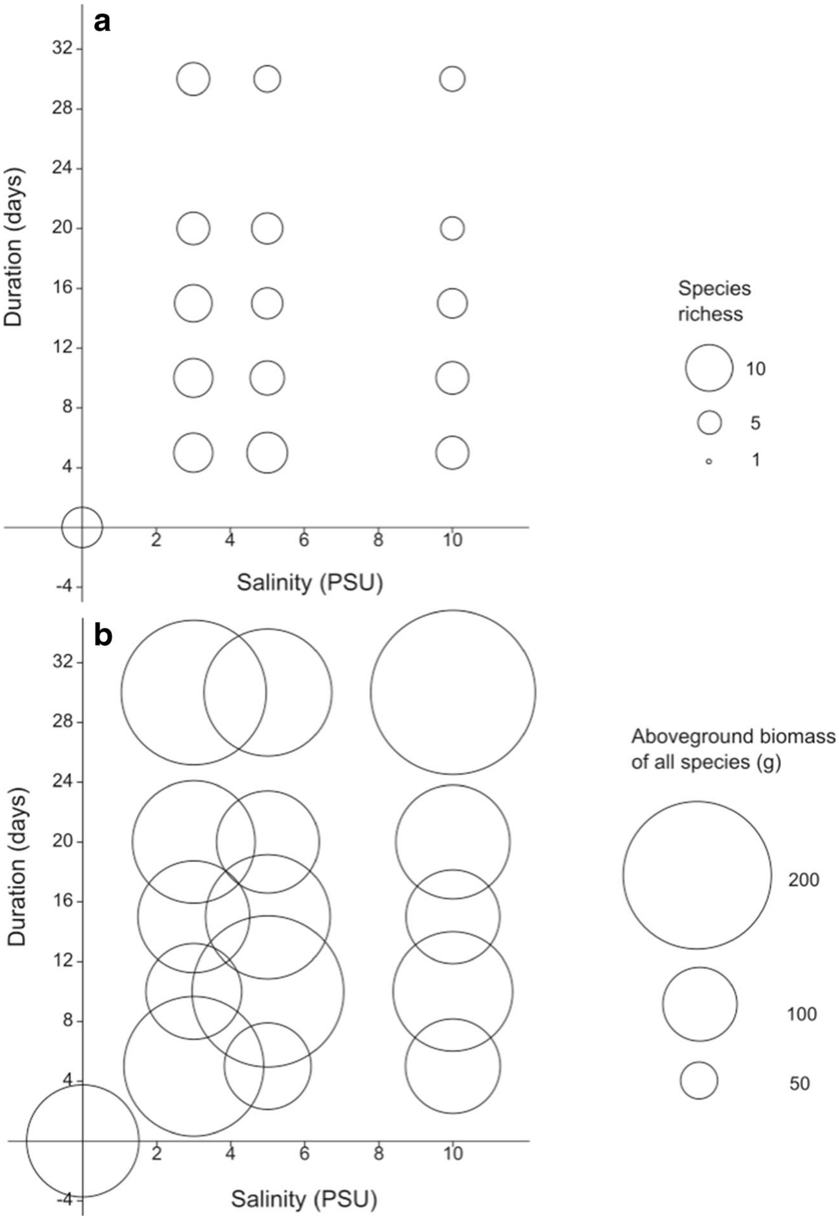

Fig. 5 Effects of exposure duration and salinity level on (a) species richness and (b) aboveground biomass of all species at the end of the treatment period (June 30, 2015). The negative effect of duration and salinity level on species richness in panel a is illustrated by smaller circles in the upper right of the figure (long duration; high salinity) than in the lower left (short duration; low salinity)

ameliorated by increased nutrient availability. In particular, porewater ammonium and phosphate concentrations were higher in the more salinized mesocosms. One mechanism increasing ammonium concentrations is likely the replacement of ammonium from soil cation exchange sites by sea salt cations (Ardón et al. 2013). Similarly, bio-available phosphate can increase with salinization due to desorption by chloride (Herbert et al. 2015). Moreover, increases in sulfate concentrations with salinization can enhance rates of organic matter mineralization through sulfate reduction (Weston et al. 2006). Finally, the high nutrient content in the more salinized treatments may also have been due to lack of uptake by plants given the lower plant biomass in these treatments. Our experiment was not designed to tease these potential mechanisms apart. Our experiment was also not designed to directly measure any potential benefit of increased nutrients due to salinization; however, Li and Pennings (2018) found that *Z. miliacea* belowground biomass increased with low-salinity pulses that lasted up to 16 days and speculated that this was due to an increase in nutrient availability in salinized treatments. Our results indicated that porewater nutrient concentrations decreased from July to August, perhaps due to increased utilization of nutrients by the salt-tolerant plants as they grew to fill the mesocosms. This possibility is consistent with the idea that saline pulses may benefit the growth of salt-tolerant plants, whereas salt-sensitive plants may be too stressed to take advantage of increased nutrient availability caused by salinization. Given the potential for salinization to benefit some plant species by making nutrients more available, future studies of seawater intrusion may benefit by closer collaborations between ecologists, biogeochemists, and plant physiologists to address this potential linkages.

Overall, results from the treatment period imply that prolonged periods of salinization will change species composition, reduce species richness, and reduce aboveground biomass in tidal freshwater marshes. Modest saline pulses may increase porewater nutrient concentrations that will support or even increase the growth of salt-tolerant species. However, if the saline conditions persist, such benefits will be overwhelmed by the negative effects of salt stress.

Despite being strongly suppressed by the salinity treatments, most of the plant species were able to recover from low-salinity, short-duration saline pulses. Although *L. repens* had the lowest salt tolerance during the treatment period, it recovered rapidly in treatments of 3 PSU water for no more than 15 days and 5 PSU water for 5 days. *L. repens* is characterized by rapid growth and spreads by lateral shoot growth to form dense mats. This ability to rapidly expand should facilitate the recovery of *L. repens* after a salinity disturbance (Rejmánková 1992). *P. hydropiperoides* was able to recover from salinization to a low abundance similar to its abundance in the control treatment. *E. palustris*, the most salt-tolerant species, became the dominant species in all experimental treatments during the recovery period. These results were consistent with previous studies indicating that a number of freshwater marsh species have the ability to recover from short-term salinity disturbances (Flynn et al. 1995; Goodman et al. 2010). Although the aboveground biomass of several of the species disappeared during the treatment period in our experiment, seeds and rhizomes of some species persisted and supported recovery when fresh conditions returned.

Reproduction by seed also allowed new species to colonize the mesocosms during the recovery period. Reproduction by seed is more common in fresh than in brackish or salt marshes (Crain et al. 2008). In our study, the seed bank survived the treatment period, and volunteer species emerged during the following year during the recovery period. The volunteers were present as seeds in the root balls of the species that we planted but did not emerge until cued to do so. Although these volunteers affected species richness and composition after the recovery period, they were relatively minor components of the community when ranked by biomass (Online resource 4) and so did not have a major impact on conclusions based on patterns of biomass.

Because of the emergence of the volunteer species, the community structure at the end of the recovery period did not overlap with that at the end of the treatment period. The communities in some of the less salinized treatments (3 PSU for 5 and 10 days, 5 PSU for 5 days) followed a similar recovery trajectory as the controls, whereas the other treatments increasingly diverged from the controls. This was largely because *L. repens* recovered in the mildly salinized treatments but remained absent in the heavily salinized ones.

At the end of the recovery period, plant aboveground biomass fully recovered in the salinized treatments despite the low species richness and was even slightly higher in the treatments that experienced longer saline pulses, possibly because the longer saline pulses made more nutrients available for plant growth. Since these treatments did not experience fluctuating conditions but instead permanent saline conditions, the more salt-tolerant species may have been able to grow steadily and offset the reduction in biomass of the salt-sensitive species. Because some of the plant species present in tidal freshwater marshes are resilient to saline pulses, plant productivity can recover from even a fairly strong and extended saline pulse in less than 1 year. Plant composition, however, may be changed by an extended saline pulse. Thus, it is likely that the species compositions of tidal freshwater marshes that do and do not experience periodic saline intrusion will differ but plant biomass may not.

Because this was a mesocosm study, it did not perfectly replicate natural conditions. The sediment depth in the mesocosms was only about 13 cm, and this may have limited growth of species that in nature root more deeply, thereby altering plant biomass and community composition in the mesocosms. We simulated only one tidal cycle per day during the treatment period of the experiment, rather than two, and we did not simulate tides at all during the recovery period. This probably affected porewater chemistry and growth of some of the plant species. Finally, although we think that most of the volunteer species were natural (i.e., the seeds came into the mesocosms with the root balls of the plants that we stocked), it is possible that some recruited from seeds produced by plants growing near the site of the mesocosm and so would not have occurred in nature. Because of these artifacts, it is likely that natural plots exposed to the salinity treatments that we used in the mesocosms would not have produced exactly the same levels of plant biomass or exactly the same community composition as we found in the mesocosms. We do think, however, that the general patterns in biomass, species richness, and species composition that we found are likely to provide insights into field patterns.

The strength of the mesocosm experiment, and the reason that we chose this approach rather than conducting a field experiment, was that it enabled us to conduct a more diverse set of treatments than it would have been feasible to conduct in the field. At the same time, as discussed above, mesocosm experiments are an imperfect replica of natural conditions. The best way to rigorously extrapolate our results to the field would be to conduct additional experiments in a natural setting, perhaps with a subset of the treatments that we studied here in order to compensate for the more complicated logistical challenges inherent in field experiments. An ongoing field experiment on the Georgia coast comparing a press and pulse saline treatment has found similar patterns of species reordering as we report here but slower recovery of salinized communities in between annual saline pulses (unpublished data).

Ecological responses to pulsed disturbance range from individual level mortality to major effects on ecosystem structure and function (Ciais et al. 2005; Smith 2011; Thibault and Brown 2008). Our study found that primary productivity was more resilient to saline disturbance than community composition. Although both species richness and productivity were reduced by salinization, the surviving species were able to regrow during the recovery period and restore total community production. Without such compensation, reductions in ecosystem function might have persisted. Therefore, changes in ecosystem structure of coastal wetlands due to global change pulses may not preclude recovery in ecosystem function.

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Author's Contributions FL and SCP conceived and designed the experiments. FL performed the experiments and analyzed the data. FL and SCP wrote the manuscript.

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