



## Resistance and resilience: Tidal freshwater marsh response and recovery to acute and chronic saltwater intrusion

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### ABSTRACT

The ability to both resist and recover from disturbances like storm surge and saltwater intrusion plays a key role in shaping the structure and function of tidal marshes. In this study, porewater chemistry, vegetation, and soil elevation change were measured in field plots of a tidal freshwater marsh exposed to four years of experimental press (chronic) and pulse (acute) brackish water additions followed by five years of recovery to assess their resistance and resilience to saltwater intrusion. Press additions produced significant, widespread changes in marsh structure and function including increased porewater N and P, reduced macrophyte cover and species richness, and loss of soil surface elevation whereas pulse additions had little effect. Once dosing ceased, porewater chemistry, vegetation and soils in press plots recovered at differing rates, with porewater N and P declining to background levels after one year, plant cover and species richness increasing within two to four years, and soil surface elevation increasing to similar levels found in control plots after five years. The plant community in the press treatment converged with the other treatments after 3–4 years, though macrophyte species exhibited varying rates of recovery. Ground cover (*Ludwigia repens*) and soft stem species (*Persicaria*) that declined first, recovered faster than *Zizaniopsis miliacea* that was more resistant but less resilient to brackish water intrusion. While tidal freshwater marshes are resistant and resilient to pulses such as those that stem from hurricanes and storm surges, continued long-term intrusion events like sea level rise (SLR) will likely lead to conversion into brackish marsh. Understanding long-term responses and tradeoffs in resistance and recovery as shown in this experiment offers insight into the future trajectory of tidal freshwater marshes as well as broader ecosystem responses to disturbance and recovery crucial to management and restoration.

### 1. Introduction

Tidal freshwater marshes are dynamic coastal wetland systems that experience highly variable hydrological regimes and have a capacity to resist and recover from these natural disturbances. Located at the nexus between marine and freshwater water sources, they are subject to predictable and unpredictable variation in inundation and salinity. Twice daily tides inundate the marsh with fresh river water while pulsed seasonal freshwater flooding and drought leads to periodic saltwater intrusion. Less predictable hurricanes, tropical storms, and storm surges can also increase marsh inundation or introduce saltwater incursion

events that can last hours to days (White and Kaplan, 2017). Resistance and resilience are pivotal attributes that determine the structure and function of tidal wetlands in the face of these disturbances.

General ecological theory defines resistance as the ability of a "system to withstand or absorb a change or disturbance with minimal alteration" (Phillips, 2018) while resilience is "the capacity to recover from the disturbance though the biota and ecological processes have been diminished" (Lake, 2013). The degree of resistance to saltwater incursion and the resilience and ability to recover from it are important in understanding how tidal freshwater wetlands, and broader coastal wetlands, will respond to current and future changes in sea level rise

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(SLR) and climate. However, there are tradeoffs between resistance and resilience that impact the susceptibility and adaptability of coastal wetlands because organisms and biogeochemical properties that are resistant to disturbance are less likely to be resilient (Patrick et al., 2022).

These tradeoffs will be tested not only in tidal freshwater marshes but other coastal wetlands as climate change is expected to lead to more frequent episodes of saltwater intrusion (Herbert et al., 2015; Wood and Harrington, 2015). Rising sea level and extended drought may produce longer lasting incursions of saltwater into coastal wetlands (Ensign and NOE, 2018). Initial impacts will likely affect coastal wetlands closest to the coast first, but will most visibly influence tidal freshwater marshes that are frequently exposed to short-term incursions of saltwater, but are less adapted to chronic, long-term salinization (Neubauer, 2013).

The impact of chronic or press saltwater intrusion on tidal freshwater marshes is well documented. Effects include reduced plant productivity and species diversity (Spalding and Hester, 2007; Delgado et al., 2018; Herbert et al., 2018; Li and Pennings, 2019; Li et al., 2022), elevated porewater salinity, sulfate and NH<sub>4</sub>-N (Weston et al., 2006; Widney et al., 2019), increased SO<sub>4</sub> reduction and depressed CH<sub>4</sub> emissions (Weston et al., 2006; Herbert et al., 2018), changes in microbial community composition including reduced diversity and C cycling (Mobilian et al., 2020), reduced soil C sequestration (Chambers et al. 2011, 2013; Ensign and NOE, 2018; Solohin et al., 2020), and soil subsidence (Charles et al., 2019; Solohin et al., 2020).

Much less is known about the short-term, acute effects of saltwater pulses, such as from storm surges or droughts. Most findings are derived from greenhouse, mesocosm, and soil core experiments rather than in-situ studies. In these experiments, plant communities are known to exhibit only slight or transient changes when exposed to short saline pulses, especially when salt tolerant plants are present (Sharpe and Baldwin, 2012; Li and Pennings, 2019). The microbial community in comparison is more sensitive to acute saline exposure though changes are temporary as increased organic carbon mineralization, sulfate reduction and reduced methanogenesis quickly reverse once pulsing ends (Chambers et al. 2011, 2013).

Direct assessment of tidal freshwater marsh resilience following disturbance events is also sparse. Only two studies were found to directly measure tidal freshwater marsh resilience, but both were less than a year in length and focused solely on vegetation (Flynn et al., 1995; Li and Pennings, 2019). Based on these two studies, concentration and duration of the salinity incursion are key factors impacting resilience. High salinities (10) have a dominant and lasting effect on vegetation recovery regardless of duration (Li and Pennings, 2019), while moderate to high salinities (5–12) in conjunction with extended inundation (15–30 days) limit recovery by slowing re-growth and species diversification that alters community composition (Flynn et al., 1995; Li and Pennings, 2019).

Beyond these mesocosm studies on vegetation, resilience, and recovery of other wetland characteristics (microbes, soils) from either acute or chronic field-based disturbances is largely unexamined despite its importance in understanding the persistence of tidal freshwater marshes in the face of rising sea level and climate change. The sustainability of other coastal wetlands will depend on a similar understanding of resilience and recovery.

This study addresses these research gaps by investigating how a tidal freshwater marsh in Georgia, USA responded before, during, and after acute (pulse) and chronic (press) saline intrusion to better understand the impacts of salinity on the persistence of tidal freshwater marshes with the goal of contributing to a broader understanding of resistance and resilience of coastal wetlands. Spanning over almost a decade of research, we built upon the work conducted at the Seawater Addition Long Term Experiment (SALTEX) (see Herbert et al. (2018), Widney et al. (2019), Solohin et al. (2020), and Li et al. (2022)) by focusing on in-situ recovery responses recorded for five years after these four-year brackish dosing studies. This study's integration of past biogeochemical, vegetation, and soil data with new recovery information provides a

novel long-term holistic examination of salinity's impacts on tidal freshwater marshes before, during, and after saline intrusion events.

We hypothesize that tidal freshwater marshes will be resistant to changes during pulsing or exhibit high resiliency by quickly recovering to control levels after dosing is ceased. We further hypothesize that tidal freshwater marshes are not resistant to chronic intrusion and exhibit significant changes in wetland biogeochemistry, plant communities and soils. Even after dosing is ceased, we expect tidal freshwater marshes under press conditions to recover slower and with a potential shift from freshwater to oligohaline plant species than when subjected to brackish pulsing.

## 2. Methods

### 2.1. Study site

The SALTEX study (Seawater Addition Long Term Experiment) was conducted in a tidal freshwater marsh on the Altamaha River in Georgia, USA. The site is inundated twice daily by astronomical tides of 2.3 m with river water that is typically fresh (~0.1). Giant cutgrass (*Zizaniopsis miliacea*) dominates the plant community along with pickerelweed (*Pontederia cordata*), smartweed (*Persicaria hydropiperoides*), and creeping primrose-willow (*Ludwigia repens*).

The experiment consisted of thirty 2.5 × 2.5 m plots arranged over a 0.1 ha area with 3 m buffers around each to minimize leakage from treatments (Appendix 1). Plots were deployed in March 2013 and were accessed from raised boardwalks to minimize trampling. Plastic polycarbonate siding (0.3 m (h) by 2.5 m (l) by 2.5 m (w)) was installed around the perimeter of each plot so that framing was 15 cm below and 15 cm above the soil surface. Two holes in the siding allowed surface water and material exchange but were plugged during dosing to retain treatment water for increased infiltration. During high tide, water flowed through holes and overtopped the siding, allowing tidal inundation of plots.

Plots were assigned to one of six blocks based on average elevation before being randomly assigned to treatment groups. Average elevation per plot was determined through measuring 4 points within each plot via a high-accuracy RTK GPS (Trimble R6; NAVD88 GEOID03; root-square mean error = 0.0037). Grouping per block occurred by organizing plots in order of average elevation before grouping the lowest six plots together into a block, followed by the next six until the last six plots consisted of the six highest in elevation.

Treatments consisted of three dosing conditions (press, pulse, and fresh) and two controls (with and without sides/framing) with six replicates each. Salinity for the treatments were initially measured in ppt during the experiment but are reported using practical salinity units throughout the paper. The press treatment simulated chronic saltwater intrusion attributed to sea level rise, receiving brackish water (~15) - created by mixing fresh river water and seawater - to achieve porewater salinity of 2.5. The pulse treatment simulated seasonal influxes of saline water experienced during storm surges or drought. These plots were dosed with brackish water during September and October to mimic periodic saltwater intrusion that often occurs during times of low river flow in the fall. During the remaining 10 months, they were dosed with fresh river water. The fresh treatment plots received freshwater from the Altamaha River to control for the effect of added water. Controls had no water additions but were subject to natural inundation by the tide. Framing around the plots may influence measured attributes (e.g. soil accretion) so a control with sides treatment was created as a procedural control to identify any impacts of the plastic siding. The second set of controls (without sides) lacked the plastic siding. Details of how treatment water was collected, mixed, and tested are given in Appendix 2.

Treatments were applied for four years, beginning in April 2014 and ending in October 2017, after the marsh equilibrated to the construction phase of the experiment for 13 months. Water treatments were applied ~four times a week during low tide when tidal water was not present on

the soil surface. An equal amount of treatment water (265 L/day) was applied to each press, pulse, and fresh plot. Framing plugs were added during dosing and removed once treatment water infiltrated the soil. After treatments were stopped, monitoring continued at the site for five years, into 2022, to observe recovery of porewater, vegetation, and soil surface elevation.

## 2.2. Measurement of wetland characteristics

Porewater was sampled every three months from 2013 to 2020. Samples were analyzed for salinity,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{PO}_4^{3-}$  (dissolved reactive phosphorus, DRP),  $\text{HS}^-$ ,  $\text{Cl}^-$ , and DOC. Detailed methods are in the supplementary materials (Appendix 3).

Percent cover of the four dominant species at the site, *Zizaniopsis miliacea*, *Pontederia cordata*, *Persicaria hydropiperoides*, and *Ludwigia repens*, was measured within the entire plot. Other subordinate species were observed in addition to the four dominant (see Appendix 4 for full list). These species were infrequent in and among plots, though they were not in the plots when the experiment was established. Thus, focus was placed on the four dominant species present at the beginning of the study. Data was reported for the month of July because this was the time of peak biomass and cover. Proportion of light penetrating the canopy was measured using a SunScan Canopy Analysis System. Again, data from summer months was reported, except in 2017 when light was measured only in October. Detailed methods are in the supplementary materials (Appendix 5).

Soil surface elevation was measured every six months (summer, winter) from 2014 to 2022 using sediment-erosion tables (SETs). SETs were installed outside but adjacent (20–30 cm) to framing of 20 of the 30 plots ( $n = 4/\text{treatment}$ ) in 2013 following methods of Cahoon et al. (2002) and allowed to equilibrate for six months before measuring. The placement of SETs outside plots was chosen to minimize disturbance to vegetation and soils. Elevated boardwalks around the plots further limited disturbance by providing access to both plots and SETs without trampling. Detailed SET methods may be found in the supplementary materials (Appendix 6).

## 2.3. Statistical analysis

Porewater variables were analyzed using three-way ANOVA with a random block design based on treatment, elevation, and sampling date, which tested for the effect of differences among the five treatments adjusting for the variation between blocks (Herbert et al., 2018). Post-ANOVA treatment means were separated using the Ryan-Einot-Welsch Multiple Range Test.

Percent cover of the four dominant macrophytes and light transmission were analyzed using repeated-measures ANOVA with elevation as a covariate to account for variation among plots. Change in soil surface elevation in response to treatments was also analyzed with repeated-measures ANOVA. Porewater and elevation data were log-transformed to meet normality assumptions for statistical analysis then back-transformed for presentation. All analyses were conducted using SAS (Statistical Analysis Systems, SAS version 9.4. SAS Institute, Cary, NC) with significance testing performed at  $\alpha = 0.05$ .

Non-metric multidimensional scaling (NMDS) visualized changes in vegetation composition over time. Bray-Curtis distances between sites were calculated from the raw species abundance data (Tebby et al., 2017). NMDS was performed in R version 4.1.0 (R Core Team, 2021) using the *metaMDS* function from the *vegan* package (Oksanen et al., 2020).

Resistance and resilience were assessed based upon statistical significance results computed from ANOVAs. Resistance was determined by the maintenance of no statistically significant difference between press/pulse and control treatments during the dosing phase. Resilience was based upon time of recovery for each variable once dosing ceased. Time of recovery was estimated by the point in time where the treatment

was no longer consistently statistically different from the sided and unsided controls.

## 3. Results

### 3.1. Porewater

Porewater chemistry was not resistant to chronic dosing with brackish water. Porewater salinity,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{PO}_4^{3-}$  (Dissolved Reactive Phosphorus, DRP), and  $\text{HS}^-$  all increased in the press treatment (Fig. 1, Widney et al., 2019). Salinity, ammonium, DRP, and sulfide rose soon after press treatment began whereas  $\text{NO}_3^-$  and  $\text{NO}_2^-$  increased some in year 1 but more so a year later in 2015. Salinity,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ , and  $\text{HS}^-$  in press plots remained elevated from other treatments during the experiment, though concentrations exhibited a gradual decline in concentration over time.

In contrast, most aspects of porewater chemistry were resistant to pulses of brackish water. Salinity increased by 1.5–2.5 during pulse dosing (Fig. 1a). Otherwise, there was little significant or prolonged effect of the pulse treatment on porewater chemistry (Fig. 1). There was no effect of either pulse or press dosing on porewater DOC (Fig. 1f).

Porewater chemistry quickly recovered from press conditions once treatments ceased. Nitrate-nitrite, while higher in non-press treatments for several years during dosing (2015–2016), converged with other treatments before dosing ended in 2017 and did not significantly differ among treatments once dosing ceased (Fig. 1e). From 2018 to 2020, nitrate-nitrite in press plots was similar to January 2014 baseline measurements (~7 g-N/L) (Appendix 7). Porewater sulfide recovered within range of the control immediately after dosing (Fig. 1c) and remained at pre-dosing levels (less than 0.5 mg S/L) (Appendix 7).

Both ammonium and DRP in the press plots recovered to control values within one year after dosing. By the fall of 2018, ammonium in all treatment groups were similar to 2014 baseline ammonium levels and remained there for the duration of the study (~4–15 g-N/L in 2020 vs ~8–18 g-N/L in 2014). DRP in the press treatment remained significantly higher than in all other treatments and controls until January 2019 (Fig. 1d). By 2020, DRP in press plots declined to 2014 baseline values of approximately 10 g-P/L (Appendix 7). DOC was variable but did not consistently statistically differ among treatments during dosing and recovery phases (Fig. 1f).

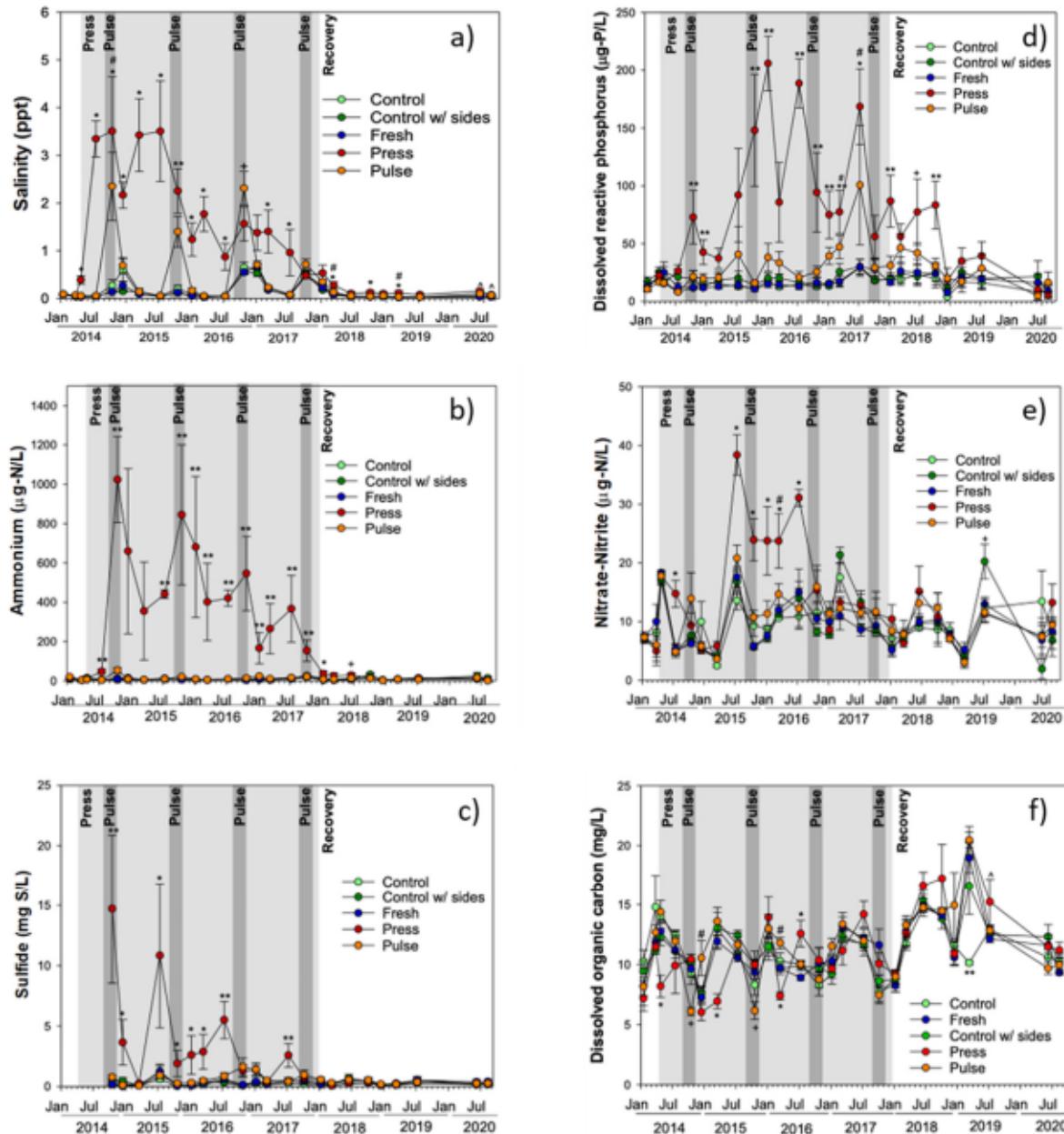
Salinity was the slowest to recover. Despite a rapid decline, once dosing ceased, salinity in the press plots remained significantly higher than the sided control (Fig. 1a, Appendix 7). Full recovery did not occur until three years after dosing ceased. At this time salinity was less than 0.1 and was not statistically significant from the control (Appendix 7).

### 3.2. Vegetation

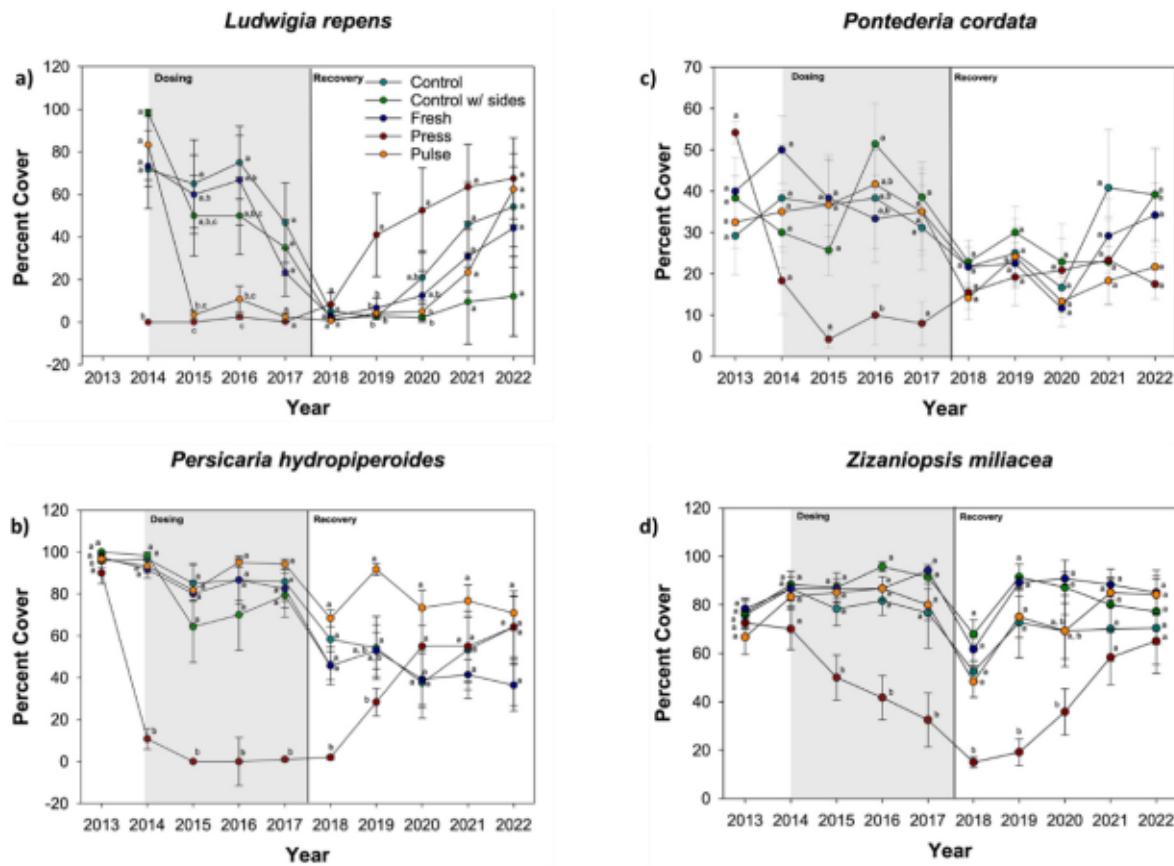
Vegetation communities were not resistant to chronic saline inundation. Cover of the four dominant plant species was significantly reduced by the press treatment (Li et al., 2022). *Ludwigia repens* was eliminated from press plots almost immediately once dosing commenced (Fig. 2a) while *Persicaria hydropiperoides* declined from 90% to 10% during the first summer of dosing (Fig. 2b). *Pontederia cordata* also declined from 55% to 18% in the first year and stayed low for the remainder of treatment (Fig. 2c). *Zizaniopsis miliacea* declined more slowly than the other species. By 2017, *Z. miliacea* in the press plots was 33% compared to 73% at the beginning of the experiment (Fig. 2d) (Appendix 8).

After one year, the plant community of the press plots diverged from control and pulse treatments (Appendix 9). At the end of the dosing phase, the press plots were distinctly different from the other treatments (Appendix 9), though they varied markedly in terms of individual species coverage.

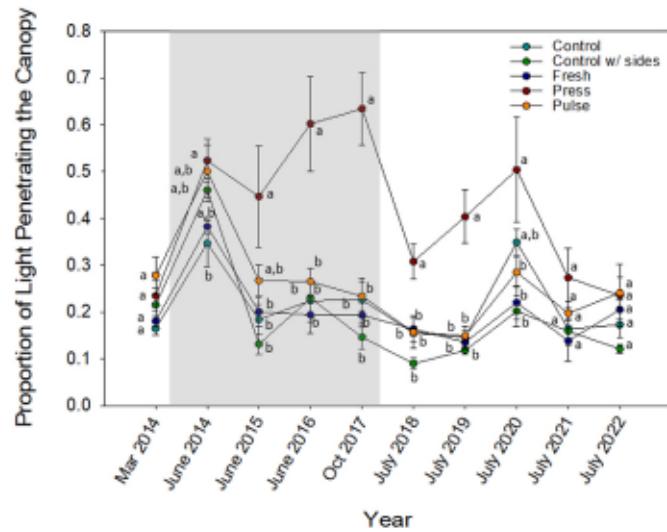
At the end of 2015, after two years of treatment additions, *Typha domingensis* and *Schoenoplectus tabernaemontani* were visually identified



**Fig. 1.** Porewater (a) salinity, (b) ammonium, (c) sulfide (d) DRP, (e) nitrate-nitrite, and (f) DOC concentrations (means  $\pm$  SE) for all plots from 2014 to 2020. Statistical symbology is as follows: \* = press significant ( $p > 0.05$ ) from other treatments (a, c, f) or press significant ( $p < 0.1$ ) from other treatments (b, d, e); \*\* = press significant ( $p < 0.05$ ) from other treatments (b, d, e) or press and pulse significant ( $p < 0.05$ ) from other treatments (a) or control significant ( $p < 0.005$ ) from other treatments (f); # = pulse intermediate to controls (C, CS, F) and press (a, c, d) or pulse significant ( $p < 0.05$ ) from press (f); + = pulse significant ( $p < 0.05$ ) from controls (C, CS, F) (a, d) or pulse significant from C and F ( $p < 0.05$ ) and CS ( $p < 0.10$ ) (b) or pulse significant ( $p < 0.05$ ) from all treatment (f) or CS significant from C, pulse, press ( $p < 0.05$ ) and fresh ( $p < 0.10$ ) (c); - = press significant ( $p < 0.05$ ) from CS and F (a) or press significant from CS and F ( $p < 0.05$ ) and C and pulse ( $p < 0.10$ ) (f).



**Fig. 2.** Percent cover of (a) *Ludwigia repens*, (b) *Persicaria hydropiperoides*, (c) *Pontederia cordata*, and (d) *Zizaniopsis miliacea* (means  $\pm$  SE) for all study plots in the month of July from 2013 to 2022. Letters signify statistical significance between treatments according to repeated-measures ANOVA. Points with the same letters are not significantly different ( $p > 0.05$ ).



**Fig. 3.** Percent of light transmitted to soil surface (means  $\pm$  SE) for all study plots in summer months from 2014 to 2022. Letters signify statistical significance between treatments according to repeated-measures ANOVA. Points with the same letters are not significantly different ( $p > 0.05$ ).

in and around the field experiment. These species were randomly distributed in and among plots at low numbers (<5%). The statistical design, (blocked ANOVA) did not detect a significant difference in these species among treatments. Over the course of the treatment additions and during recovery, there was no marked increase or change in these species in the press or pulse treatment compared to the fresh and control treatments.

*L. repens* was the only species affected by the pulse treatment as it declined from 83% to 3% between years 1 and 2 of dosing (Fig. 2a). Cover of *L. repens* remained low for the duration of dosing, but it never fully disappeared from the plots. *L. repens* maintained declines in all treatment plots going into 2018 as the storm surge from Hurricane Irma made landfall in September 2017 (see section 4.3 Confounding factors).

Loss of vegetation in the press plots led to increased light reaching

the soil surface (Fig. 3, Li et al., 2022). By 2017, press plots on average had almost 65% of light penetrating the canopy compared to 15–23% in the other treatments, which remained relatively constant year to year during dosing (Appendix 10).

The press treatment, which had dramatic reduction in species cover during the dosing phase, began to recover once dosing ceased. Cover of *L. repens* and *P. cordata* were statistically similar to control plots once dosing ceased. This outcome was attributed to loss of these species in all plots due to Hurricane Irma's storm surge (Fig. 2a and c). *L. repens* quickly increased from its near eradication during dosing as press plots received greater light penetration early in the recovery period compared to other plots. Four years after dosing ceased, *L. repens* coverage was not significantly different than the control plots that exhibited slower recovery (Appendix 8).

Like *L. repens*, *P. hydropiperoides* recovered quickly and converged with control plots by 2020 (Fig. 2b). Recovery of *Z. miliacea* in press plots was the slowest compared to the other species (Fig. 2d). By the fourth year (2021) coverage was not statistically significant from the other treatments (Fig. 2, Appendix 8).

During the five-year recovery period, the plant community in the press plots converged with the other treatments (Appendix 9). However, final species cover varied from pre-dosing values. By the fifth year of recovery, cover of *P. cordata* was 20%, much lower than that of the pre-dosing baseline (55%) (Appendix 8). *P. hydropiperoides* was also lower than pre-dosing baseline (Appendix 8). In contrast, *Z. miliacea* recovered to levels similar to pre-dosing measurements (65% in 2022 vs 72% in 2013).

*L. repens* was the only species affected by the pulse treatment. Cover remained low for the first three years of recovery but accelerated soon after. By 2021 cover was similar to the control and other treatments though it was less (62.5%) than the 2014 baseline (83%).

All species in non-press plots declined in 2018 owing to the effects of Hurricane Irma's storm surge, but quickly recovered (Appendix 8). After five years, *P. hydropiperoides* and *P. cordata* in pulse plots regained close to original 2014 levels (71% vs 97% and 22% vs 32% respectively) while *Z. miliacea* had greater coverage (84% vs 67%).

As vegetation recolonized the press plots, light transmission to the soil surface decreased from 63% to 31% after one year (Fig. 3). In contrast, the other treatments had minimal change in light transmission during this time (1–8% decline). After five years, light transmission was similar in all treatments, converging on pre-dosing measurements of 12–24% light reaching the soil surface (Appendix 10).

### 3.3. Elevation

Soil surface elevation declined over time in response to press dosing (Fig. 4, Solohin et al., 2020). After four years, elevation in press plots declined by 25 mm while control, control with sides, and fresh treatments gained elevation (18 mm, 19 mm, and 24 mm respectively). The pulse treatment neither gained nor lost elevation (~3 mm total gain) during the experiment; and after two years of dosing, its elevation was significantly different from both the press, the control, and other treatments (Fig. 4).

All treatments gained elevation during the recovery period (Fig. 4). After one year (January 2018–December 2018), press plots gained 3.8 mm of elevation. By the end of year two, soil surface elevation increased an additional 9.6 mm. In years three and four, elevation gain continued with a rise of more than 10 mm each year.

Pulse plots, which neither gained nor lost elevation during dosing, began to build elevation soon after dosing ceased (Fig. 4). By the end of 2018, elevation gain was 4 mm, with increases of 5–9 mm in annual elevation capital through 2020. As during the dosing phase, the fresh and two control treatments continued to consistently gain elevation, with annual increase for the control, control with sides, and fresh being 1–4 mm, 10 mm, and 4–8 mm, respectively.

After 5 years of recovery, all plots converged to elevations that were not significantly different from one another, (Fig. 4). Press plots had the largest total cumulative elevation gain during recovery from 2018 to 2022 (50.6m) followed by the control with sides (41 mm), fresh (29.3 mm), pulse (23.3 mm), and control (20.5 m) treatments. The control with sides saw the largest cumulative elevation gain by the end of 9 years (60 mm) when compared to the starting elevation followed by the fresh (54 mm), control (38 mm), pulse (29 mm), and press (27 mm) treatments.

## 4. Discussion

Our field experiment suggests that tidal freshwater marshes are resistant to acute but not long-term saline inundation. Yet chronic saltwater intrusion is becoming more common with the rise in sea level and changing duration of drought and flooding regimes (Tully et al., 2019). The timescale of recovery produced by this study offers novel insights to better understand the ability of tidal freshwater marshes to resist and recover from chronic versus acute saline pressures, including important implications for their persistence that can be applied to broaden understanding of ecosystem resistance and resilience in coastal

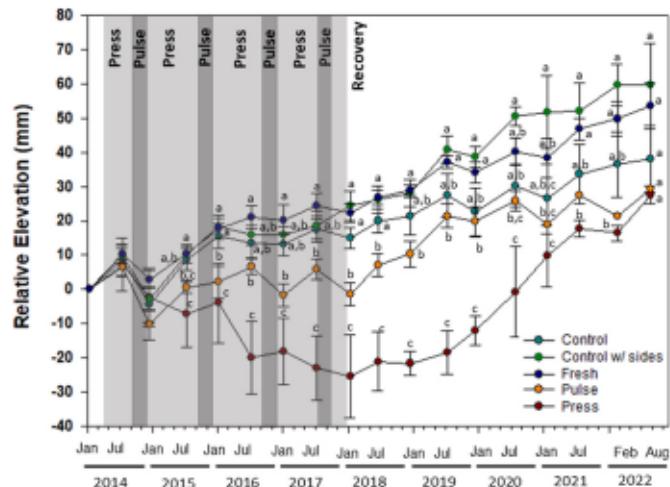


Fig. 4. Relative change in elevation pre and post treatment from 2014 to 2022. Initial conditions were set at zero to display changes during dosing and recovery. Letters signify statistical significance between treatments according to repeated-measures ANOVA. Points with the same letters are not significantly different ( $p > 0.05$ ).

wetlands.

#### 4.1. Resistance to saline intrusion

Results from the press treatment showed that these marshes were not resistant to chronic brackish water intrusion with a porewater salinity of 2–5. Herbert et al. (2018) and Widney et al. (2019) showed rapid increases in inorganic N and P and sulfide within porewater along with declines in total and individual macrophyte species abundance (Li et al., 2022) and loss of soil surface elevation (Solohin et al., 2020) (Figs. 1–3). In contrast, porewater and vegetation in the pulse treatment were generally resistant to brackish water pulsing, with little to no prolonged statistical differences (Appendix 7 and 8).

Soil physicochemical properties that drive porewater biogeochemistry generally are not resistant to brackish water intrusion. Increased porewater  $\text{NH}_4^+$  that is often observed in response to saltwater intrusion (see Chambers et al., 2013; Weston et al., 2006; Jun et al., 2013; Osborne et al., 2015) may be attributed to displacement by sodium ( $\text{Na}^+$ ) and other seawater cations. Displacement of ammonium from cation exchange sites can reduce porewater stability by shifting microbial nitrate metabolism from denitrification to nitrate reduction to ammonium (Herbert et al., 2018; Widney et al., 2019). Increased porewater DRP is also driven by soil physiochemistry, especially iron, as anaerobic conditions promote the formation of Fe sulfides, Fe(III) reduction, and the dissolution of Fe-P (Jordan et al., 2008; Kinsman-Costello et al., 2023).

Porewater  $\text{NO}_3^- + \text{NO}_2$  increased in press plots but there was a consistent lag time of about one year after porewater  $\text{NH}_4^+$  increased (Fig. 1). This lag could be conceivably attributed to increased nitrification in response to increasing porewater  $\text{NH}_4^+$ . When nitrification-denitrification is highest during the summer months (Hamereley and Howes, 2005), porewater nitrate in our study was also highest (Fig. 1c). This coupling suggests that porewater-ammonium driven nitrification could cause the eventual increase in porewater nitrate observed in the press treatment. Herbert et al. (2020) suggests a similar phenomenon in their long-term fertilization experiment on the marsh from this study where porewater nitrification potential was positively correlated with ammonium concentrations ( $p = 0.971$ ,  $p < 0.0001$ ).

Chronic brackish water intrusion also hinders microbial resistance and diversity. Mobilian et al. (2020) reported a decrease in  $\alpha$ -diversity of microbial communities in response to press treatment along with a decline in carbon extracellular enzyme activity. In contrast, pulse plots retained both microbial diversity and ecosystem functionality compared to press treatment despite observed changes. Increases in sulfate within pulse plots were largely transient (Widney et al., 2019). Potential sulfate reducing microbes also increased in pulse plots relative to fresh and control treatments (Mobilian et al., 2020) but there was little functionally significant effect as porewater sulfide concentrations were not

affected (Widney et al., 2019).

Salinity tolerance, especially duration, may explain the difference in plant resistance to pulse and press inundation. All four species declined or were nearly eliminated (*Ludwigia*, *Persicaria*) under press conditions. Mesocosm studies report similar declines under long duration (three-six weeks) of salinity incursion at both low (3) and high salinity (5–15) and under exposure to short duration (1 week) at high salinity (10) (Flynn et al., 1995; Li and Pennings, 2019). Overall, the mesocosm studies and our field experiment both ranked the species similarly in terms of their resistance to salinity, with *Zizaniopsis miliacea* showing more resistance than *L. repens* and *P. hydropiperoides*.

*Ludwigia repens* was the only species to decline during pulsing. This outcome may be attributed to *L. repens*' greater vulnerability to brackish inundation as a groundcover species whose shoots are fully submerged at high tide. Collectively, our field experiment and published mesocosm studies support the idea of species-specific thresholds where, beyond a certain duration and level of salinity, tidal freshwater marsh plants are no longer resistant to salinity incursion.

Several new species were also observed in low, inconsistent abundance across plots during the dosing phase (Appendix 4). These species were not present when the experimental design was implemented in 2013 nor before treatments were initiated. In particular, *Typha domingensis* and *Schoenoplectus tabernaemontani* were first observed in 2015, two years after dosing began. The two species were observed in low density (<5%) in some press plots as well as in and around other plots. The patchy distribution and low abundance of these two species did not permit us to statistically test whether they responded to treatment additions. However, both species are found in brackish and well as freshwater habitats (Bansal et al., 2019; Batistel et al., 2022). So, it is possible that press (and pulse) salinity additions and some leakage of treatment water from the plots contributed to their appearance.

Resistance to soil elevation change is likely tied to vegetational changes. The loss of vegetation, especially the root mat, could explain dramatic elevation decline in the press plots since it plays an important role in maintaining elevation (Kirwan et al., 2010; Wasson et al., 2019; Solohin et al., 2020). In our experiment, Solohin et al. (2020) found that the press plots contained half the belowground biomass ( $1631 \text{ g/m}^2$ ) found in the control treatments ( $2964 \text{ g/m}^2$ ). Growth of new roots into press plots was also severely reduced (Solohin et al., 2020). In contrast, pulse plots neither gained nor lost elevation while control treatments gained elevation during the 4 years of dosing. Lack of elevation gain in the pulse treatments was not due to reduced belowground biomass (Solohin et al., 2020) but was likely the result of declines in the groundcover species *Ludwigia* (Fig. 2).

The importance of biomass in elevation responses applies broadly to coastal wetlands. The biomass-driven loss of elevation observed in the press plots during dosing is expected for organic-rich tidal freshwater

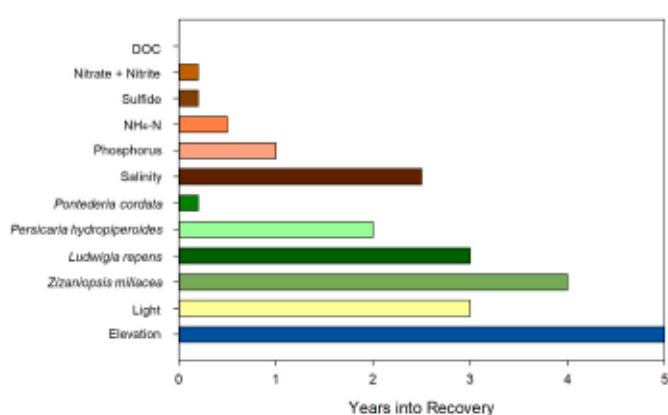


Fig. 5. Recovery Timeline for Tidal Freshwater Marsh after Chronic Saline Intrusion. Each bar signifies length in time for wetland properties to reach study's standard of recovery where treatment was similar to control.

marshes. However, root inputs impact the process of elevation gain in saline tidal marshes, too. [Morris and Sundberg \(2024\)](#) reported that in salt marshes of North inlet South Carolina, soil elevation gain was driven by root production, biomass, and organic matter accumulation.

#### 4.2. Resilience to saline intrusion

Whereas tidal freshwater marshes were largely resistant to acute brackish water intrusion as shown by our results, they were not resistant to chronic inundation. But, once dosing ceased, they recovered – albeit different components (porewater, vegetation and soil surface elevation) recovered at different rates ([Fig. 5](#)).

Porewater constituents, which increased immediately during the first year of dosing, recovered quickly. Within one to two years after dosing ceased, inorganic N and P and sulfide concentrations were within their original ranges and similar to the controls ([Fig. 1](#)). The rapid response observed in porewater could be attributed to recovery of nutrient cycling processes by the microbial and vegetation community once dosing ceased. With the cessation of brackish water dosing, microbial sulfate reduction declined as sulfate inputs driving the reaction decreased. The absence of sulfate inputs also likely reduced desorption of P from Fe-P minerals. Finally, as vegetation recolonized the plots, inorganic N decreased as the newly growing vegetation assimilated porewater N ([Widney et al., 2019](#)).

Resiliency of vegetation depends not only on reintroduction of freshwater, but also on leaching of existing salinity in porewater. Vegetation cover in press plots began to increase in the 2019 2020 growing seasons, more than a year after porewater recovery, as salinity declined and approached background levels. A one-year mesocosm study by [Flynn et al. \(1995\)](#) similarly found that success of vegetation recovery depended on reductions in porewater salinity after chronic inundation with brackish water.

Disparities in *L. repens* recovery between the controls could be explained by this impact of salinity on vegetation. Plastic framing in the study held water within plots. Retention of brackish water from storm surges, including in 2017, could have exposed ground species such as *L. repens* to longer saline stress, thereby reducing recovery in sided plots compared to non-framed plots ([Fig. 2a](#)).

It is unclear why *L. repens* density continued to remain low in the sided versus the non-sided control years into recovery ([Fig. 2](#)). It is unlikely residual salinity due to possible siding-induced water retention was a factor given porewater salinity was not significantly different between sided and unsided plots by June 2019 ([Appendix 7](#)). While shading may play a factor as there was lower light penetration in the framed plots ([Appendix 10](#)), the difference in light was minimal and likely not the main factor driving this change. Further study on this species may offer more insight into this species recovery response.

Recruitment and marsh seedbanks play a pivotal role in shaping community recovery responses. [Flynn et al. \(1995\)](#) found that the presence of freshwater marsh seeds in transplanted sod led to biomass recovery of freshwater marsh vegetation after exposure to high salinization compared to brackish marsh vegetation which lacked seeds in the seedbank. In our 9-year experiment, the four macrophyte species still dominated as there was little recruitment of new species and minimal compositional difference in the plant community following disturbance ([Appendix 9](#)). The few species introduced during the dosing phase ([Appendix 4](#)), including *T. domingensis* and *S. tabernaemontani*, did not increase in abundance over time during the remainder of the dosing and recovery phases. It is likely that a four-year intermittent (weekly) dosing disturbance (with regular inundation with freshwater river water between doses) was not sufficient to drive lasting, wholesale change in the tidal freshwater marsh, a community that is adapted to periodic salinity incursions during storms.

Plot design may also affect the rate of recovery or brackish conversion. The plot size may slow recruitment and vegetative colonization in larger plots and isolated mesocosm like [Li and Pennings \(2019\)](#). Plastic

framing around the plots could serve as a barrier to colonization by physically preventing infiltration. However, seedbanks could reduce this limitation as they hold a greater role in both recruitment and recovery in fresh and low-salinity marshes ([Crain et al., 2008](#)). Limitations on brackish conversion due to frames may result from these species dependency on the presence of vegetation runners for colonization ([Crain et al., 2008](#)), though recurring flushing of daily fresh river water, presence of live roots of freshwater species, and potential slowing of invasion by freshwater seedlings from the seedbank ([Crain et al., 2008](#)) likely played more of a factor in conversion prevention. Furthermore, the control plots within our experiment show the frame's effect on vegetation was minimal for they shared similar species composition at the end of the study ([Appendix 8 and 9](#)).

Species tolerance to salinity may also play a role in vegetation recovery. Typical vegetation communities found in tidal freshwater marshes are diverse, with species salinity tolerance being both variable and flexible to an extent. Though *Ludwigia repens* declined faster than other species, it also recovered faster. We attribute some of this to greater light reaching the soil surface due to reduced competition from the other three dominant emergent species ([Fig. 3](#)). As *L. repens* cover increased during recovery, light transmission in press plots declined from roughly 60% 30% after one year, but it was still greater than in other treatments ([Appendix 10](#)). *Persicaria hydropiperoides* that was also not resistant to brackish water intrusion displayed higher resiliency as it began to recover after two years (2019) while the more resistant, clonal dominant, *Zizaniopsis miliacea*, did not exhibit increased cover until the 2020 growing season. In contrast, *Pontederia cordata* showed little evidence of recovery during the five years after dosing ceased ([Fig. 2, Appendix 8](#)).

Other studies have found differential recovery responses among tidal freshwater marsh species ([Flynn et al., 1995](#); [White and Alber, 2009](#); [Li and Pennings, 2019](#)). Few have focused on the dominant species within our study, but [Li and Pennings \(2019\)](#) made a similar observation with our four focal species. In their year-long mesocosm experiment, *L. repens* was also the fastest to recover compared to *Z. miliacea*, *P. cordata*, and *P. hydropiperoides* despite experiencing near extirpation and having low tolerance as observed in our experiment.

Tradeoffs between resistance and resilience may explain the species-specific variation observed in response to intrusion (e.g., *Z. miliacea* having slower rate of loss and recovery compared to *P. hydropiperoides* which declined quickly but also recovered quickly). Our findings regarding this balance between resistance and resilience agree with the synthesis study of [Patrick et al. \(2022\)](#). In a meta-analysis of 118 locations of varying ecosystem types in the Atlantic basin during 26 different storms from 1985 to 2018, [Patrick et al. \(2022\)](#) documented the tradeoff in vegetational response between resistance and resilience to disturbance. Vascular wetland plants tended to have lower resilience but high resistance to factors such as wind speed and rainfall. Similarly, for freshwater systems examined, biogeochemistry that included nutrients, trace elements, and microbes exhibited low resistance to wind and rain but high resilience. This tradeoff can be scaled down to the species level where, over evolutionary time, species typically pursued either resistance or resilience strategies ([Patrick et al., 2022](#); [Miller and Chesson, 2009](#)).

Differences in species resistance and resilience to chronic saline intrusion have implications for future community composition. Most of the species observed did not regain original coverage levels. Some species (e.g., *L. repens*, *P. hydropiperoides*) continued to increase in coverage, suggesting more time was needed to observe full recovery. Other species (e.g., *P. cordata*) exhibited stagnant growth as controls regained similar baseline conditions. Only *Z. miliacea* reached similar pre-dosing percentages after dosing, but only after five years of recovery from press conditions. The multi-year lag in response to chronic salinization by some species (e.g., *Persicaria*, *Zizaniopsis*, *Pontederia*) may open the door to immigration of new species (e.g., the two brackish species, *Typha domingensis* and *Schoenoplectus tabernaemontani*, observed in the study)

or release of subordinate species (e.g., *Iris* sp. or *Pluchea* sp.), altering the trajectory of tidal freshwater marsh vegetation communities. Furthermore, effects of salinity on seed germination could further lead to compositional changes in community structure (White and Alber, 2009). The effects of salinity on recruitment as well as species specific responses to it may result in a lasting change in community composition and function such as dominance of more saline tolerant species, reduced plant diversity, and reduced importance of seeds in colonization and recruitment.

Soil surface elevation was the slowest attribute to recover from chronic intrusion of brackish water. This lag may be attributed to the need for vegetation to re-establish first before contributing to elevation gain. As the dominant vegetation began to recover, relative elevation also began to increase immediately (2018) in the pulse treatment and two years later (2020) in the press treatment (Fig. 4). By 2021, elevation in press treatments surpassed pre-dosing values and were within range of the controls whose elevation increased throughout the experiment (Fig. 4). The pulse treatment saw slower rates of elevation gain compared to press treatments during recovery, but this could be attributed to less loss of elevation capital during dosing (Fig. 4) and hence less capital to recuperate during recovery compared to the press treatment.

Plastic siding around plots may have also aided elevation gain observed in the study. The control with sides had greater elevation gain compared to the control without sides. Yet, throughout the experiment, this increase was not significant from the freshwater or unsided control (Fig. 4). Siding may still have some impact on elevation by sheltering the SETs, acting as a baffle to trap sediment. However, we did not distinguish between elevation gain due to sediment trapping versus in situ gain from roots and rhizomes which is the major driver of soil accretion in tidal marshes.

#### 4.3. Confounding factors

Our dosing experiment was truncated by Hurricane Irma in September 2017 which had some lingering effects on measurements following the storm. Between September 11–13th 2017, Irma skirted the Georgia coast with winds of 93 kph and gusts up to 124 kph (Cangialosi et al., 2021). A storm surge of 1–2 m introduced saltwater up the Altamaha River channel. River salinity at the Georgia Coastal Ecosystem (GCE) site 9, located 0.5 km upstream of the experiment, increased to 22 before declining to typical freshwater levels after 48 hours (Smith et al., 2024).

Legacies from saltwater incursion produced by the storm surge – which increased porewater salinity in all plots one month later to roughly 0.5–0.7 (Appendix 7) could explain the 30% decline in macrophyte cover across all species between 2017 and 2018 for all treatments (Fig. 2, Appendix 8). Three to four months after the storm, porewater decreased to original ranges as salinity declined to 0.2–0.3 in non-press plots (Appendix 7). Despite this unplanned, experiment-wide incursion of brackish water, the four species in all treatments displayed similar recovery trajectories in treatment plots with *Ludwigia* recovering first, followed by *Persicaria*, then *Zizaniopsis* (Fig. 2, Appendix 8).

Hurricane Irma's lack of impact on elevation despite its reduction of vegetation can be attributed to the timescale of its impact. Hurricanes produce surges that create short-term salinity spikes. The acute salinization kills above ground vegetation, but is not lasting enough to completely kill plants. Belowground biomass and roots survive (Solohin et al., 2020) and, as aboveground vegetation regrows, accretion accelerates. After five years of recovery, elevation gain is comparable to plots that were not exposed to salinity. However, long-term salinization that would occur with sea level rise would be expected to lead to a shift from freshwater to brackish species that may or may not be able to maintain elevation gain.

Shifts in tidal freshwater marsh plant communities over time as seen in our study are to be expected. Odum et al. (1984) highlights seasonal

shifting of tidal freshwater marsh vegetation as well as migration in response to environmental factors like drought and salinity. Our long-term experiment tracking disturbance and recovery lends support to the idea that both chronic and acute disturbances, especially from brackish and saltwater intrusion, shape tidal freshwater marsh communities as species abundance and composition change over time. Thus, one wouldn't necessarily expect to see species recover to pre-dosing levels of nine years earlier.

The plant community of treatment plots was similar to those prior to dosing, but there were differences in abundances as shown by the density of clustering in 2013 versus 2022 (Appendix 9). The press treatment displayed the most relative change in cover from 2013 to 2022 with decreases in *Persicaria* and *Pontederia*, though we also observed changes in the pulse plots most notably lower *P. hydropiperoides* and higher *Z. miliacea* cover (Appendix 8). However, non-treatment plots (control, control with sides, and fresh) also saw shifts in relative abundance of the four dominants. Between July 2013 and July 2022, *L. repens* and *P. hydropiperoides* were significantly less abundant in 2022 compared to 2013/2014 while *Z. miliacea* and *P. cordata* saw no change (Appendix 8). The subtle but changing composition of plant communities in all plots over time reflects the potential impact of natural acute occurrences of these salinity incursions that may vary year to year depending on river discharge and occurrence of tropical cyclones.

#### 5. Conclusions

Our nine-year field experiment shows tidal freshwater marshes are both resistant and resilient to natural pulsed brackish water intrusion but are not resistant to chronic salinization. Complete recovery after cessation of press intrusion is possible, but not rapid (Fig. 5). Porewater chemistry returned to pre-dosing conditions quickly while vegetation took years, with surface elevation the last to recover. Though tidal freshwater marshes are currently able to resist periodic saline intrusions, prolonged events like SLR or extended drought may lead to ecosystem changes that have been shown to cause conversion from freshwater to brackish marsh.

Tidal freshwater marshes offer a window to understand the factors involved in ecosystem disturbance responses given their regular exposure to saline intrusions. The interplay between resistance and resilience observed within this tidal freshwater marsh experiment can inform disturbance frameworks important in the management of coastal ecosystems. As managers and decision makers seek to increase resistance and resilience of coastal marshes (Patrick et al., 2022), our results demonstrate the tradeoffs, variable sensitivity to disturbance, and sequential patterns of recovery that should be used to guide efforts in successfully conserving or restoring these ecosystems.

#### CRediT authorship contribution statement

**Madeleine F. Thompson:** Writing review & editing, Writing original draft, Visualization, Formal analysis. **Steve C. Penning:** Writing review & editing, Investigation, Formal analysis, Conceptualization. **Joseph P. Schubauer-Berigan:** Writing review & editing, Investigation, Formal analysis. **Ellen R. Herbert:** Writing review & editing, Investigation, Formal analysis, Conceptualization. **Galen Costomiris:** Software, Formal analysis. **Christopher B. Craft:** Writing review & editing, Investigation, Formal analysis, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

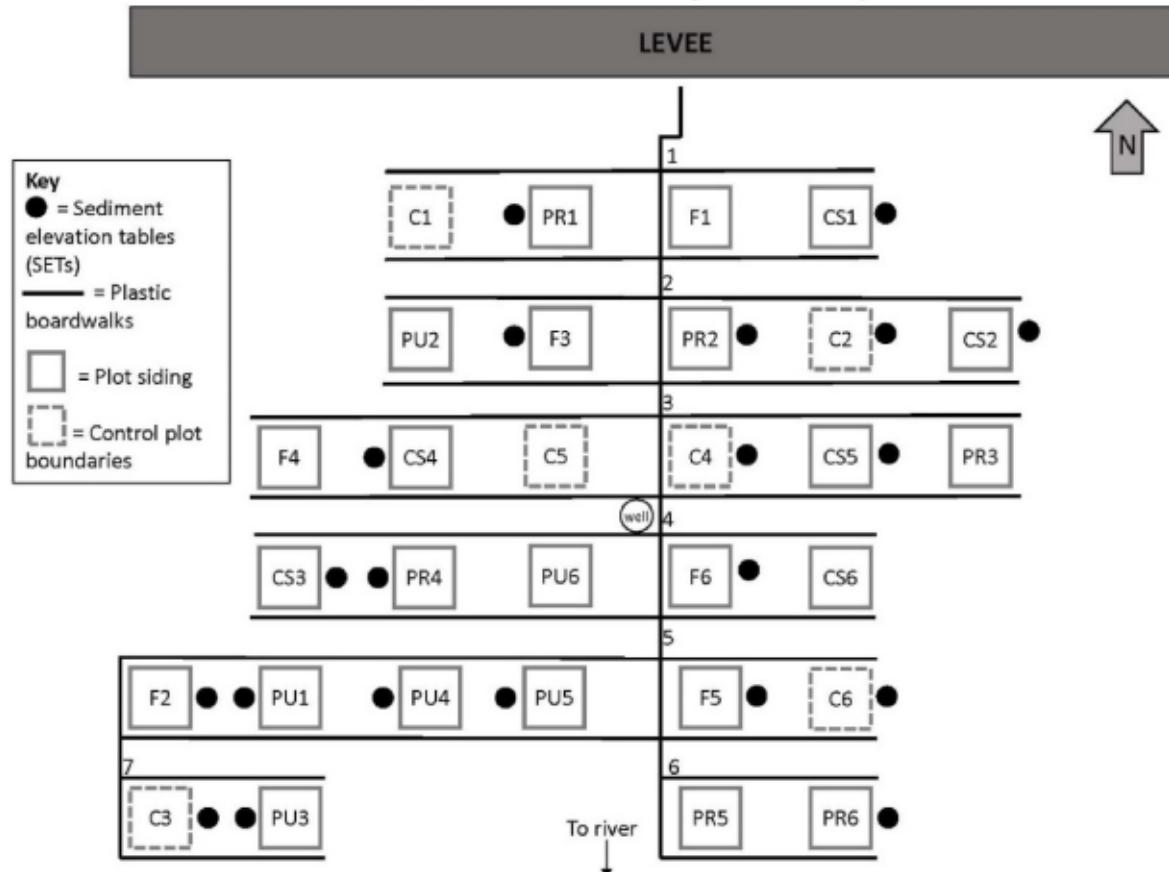
Data presented in this paper is available in the Georgia Coastal Ecosystem (GCE) database which can be accessed on the GCE-LTER catalog site via the following DOI links: porewater ([10.6073/pasta/045ad069c3bf253d7bd81fdff2f5664](https://doi.org/10.6073/pasta/045ad069c3bf253d7bd81fdff2f5664)), vegetation ([10.6073/pasta/554fb232ea0ae95144f0857a604e73c](https://doi.org/10.6073/pasta/554fb232ea0ae95144f0857a604e73c)), light ([10.6073/pasta/1c78ffbb1d1419fcc50cb1892f3c3191](https://doi.org/10.6073/pasta/1c78ffbb1d1419fcc50cb1892f3c3191)), and SET ([10.6073/pasta/bd27073074035d008a43781f0501df7d](https://doi.org/10.6073/pasta/bd27073074035d008a43781f0501df7d))

## Acknowledgements

We thank everyone who helped conduct research at SALTEX. We

## Appendix 1. Image of study design and site configuration at the emergent tidal freshwater marsh in Macintosh County, Georgia, USA

### Experimental Design and Layout



## Appendix 2. Treatment Water Methods

Fresh treatment water is taken from the Altamaha River and filtered before being applied. Press and pulse brackish treatment water was created through mixing filtered (50  $\mu\text{m}$  nominal pore size) seawater collected from a tidal creek in Meridian, GA, and Altamaha River water near the SALTEX into opaque tanks to reach a salinity of 15. Water sources were analyzed between January 2016 and March 2017 to determine chemical composition (see Treatment Water Table below). Compared to river water, seawater had higher salinity (22 vs 0.09) and sulfate (1914 mg/L vs 36 mg/L) but nitrogen ( $\text{NH}_4$ ,  $\text{NO}_3^-$ , total N), phosphorus (total P), and dissolved organic carbon were higher in river water. Brackish water that was used during treatments was intermediate to the two source waters.

Treatment Water Table. Mean SE (number of samples analyzed).

Water type	Salinity (ppt)		NH <sub>4</sub> ( g-N/L)		NO <sub>3</sub> <sup>2</sup> ( g-N/L)		PO <sub>4</sub> ( g-N/L)		Total N ( g-N/L)		Total P ( g-N/L)		SO <sub>4</sub> <sup>2</sup> (mg-N/L)		DOC (mg-N/L)	
Sea water	21.88 (5)	1.93	14.95	5.03 (5)	17.22	1.62 (5)	55.94 (5)	7.50	673.4	98.3 (5)	71.86	8.84 (5)	1914 (2)	12 (2)	6.12	0.56 (5)
River water	0.09 (6)	0.03 (5)	56.78 (6)	19.76	199.3 (6)	39.06	46.43 (6)	8.28	1265	243 (6)	142.6	52.1 (6)	36 (6)	6.9 (2)	13.14 (6)	2.70
Treatment water	16.24 (5)	0.08	29.93	2.60 (6)	98.46 (6)	19.52	52.62 (6)	5.53	741.0	54.4 (6)	60.46	5.07 (6)	1546 (2)	116	8.27	1.18 (6)

### Appendix 3. Porewater Methods

Porewater was sampled seasonally every three months from 2013 to 2020, with the recovery sampling phase spanning 2018–2020. During each sampling period, two wells per plot were randomly selected and purged before sampling. Measurements were conducted at least two tidal cycles (~24 h) after the most recent water treatment application and 30 min after purging the well. Water from each well was combined into a 500 ml acid-washed Nalgene bottle. 20 ml of composite water was transferred to a 50 ml centrifuge tube with Orion sulfide antioxidant buffer (SAOB) for sulfide analysis. Samples were processed and frozen prior to analysis as described in [Widney et al. \(2019\)](#).

Samples were analyzed for salinity, NH<sub>4</sub>, NO<sub>3</sub>–NO<sub>2</sub>, PO<sub>4</sub> (dissolved reactive phosphorus, DRP), HS, Cl, and DOC. The US EPA Office of Research and Development (Cincinnati, OH) conducted analysis of N and P using a Lachat QuikChem 8500 Flow Injection analysis system. Indophenol blue complex (QuikChem method 10-107-06-1-B), cadmium reduction/EDTA red complex (QuikChem method 10-107-04-1-J), and molybdate blue complex were used for NH<sub>4</sub>, NO<sub>3</sub>–NO<sub>2</sub>, and PO<sub>4</sub> measurements, respectively.

Salinity, Cl, SO<sub>4</sub><sup>2</sup>, HS, and DOC analyses were performed at Indiana University. Measurements for Cl and SO<sub>4</sub><sup>2</sup> were gathered using a Dionex ICS-2000 Ion Chromatograph (Sunnyvale, CA) with an AS11-HC analytical column. Analysis of HS was conducted with the Orion Model 9616 Sure-Flow Combination Silver/Sulfide Electrode with Optimum Results B filling solution. DOC was measured using a Shimadzu TOC-V<sub>cpn</sub> analyzer. Ultrapure deionized water blanks were run in each analysis every 10 samples to correct any instrumental drift. See [Herbert et al. \(2018\)](#) and [Widney et al. \(2019\)](#) for detailed methodology on porewater analysis.

### Appendix 4. SALTEX Plant List

Below is a list of plants that were observed in and around the SALTEX experiment during the summer of 2017, before the Hurricane Irma storm surge in September. The first four are the dominant vegetation that were used in vegetational analysis. *Typha domingensis* and *Schoenoplectus tabernaemontani* were the two brackish species observed in some of the plots beginning in 2015.

Scientific Name	Common Name
<i>Ludwigia repens</i>	Creeping primrose-willow
<i>Zizaniopsis miliacea</i>	Giant cutgrass
<i>Pontederia cordata</i>	Pickerelweed
<i>Persicaria hydropiperoides</i>	Swamp smartweed
<i>Sagittaria lancifolia</i>	Arrowhead
<i>Pluchea</i> sp.	Camphorweed sp.
<i>Epilobium</i> sp.	Willowherbs
<i>Cyperus haspan</i>	Haspan flatsedge
<i>Carex</i> sp.	Sedges
<i>Iris</i> sp.	Iris
<i>Cuscuta</i> sp.	Dodders
<i>Agalinis linifolia</i>	Flaxleaf false foxglove
<i>Elocharis</i> sp.	Spikerushes
<i>Peltandra virginicus</i>	Green arrow arum
<i>Schoenoplectus tabernaemontani</i>	Softstem bulrush
<i>Typha domingensis</i>	Southern cattail

### Appendix 5. Vegetation Methods

Percent cover of four site-dominant species, *Zizaniopsis miliacea*, *Pontederia cordata*, *Persicaria hydropiperoides*, and *Ludwigia repens* within the entire 2.5m × 2.5m plot was estimated roughly four times a year from 2013 to 2022, though measurements of *L. repens* began in 2014. Visual estimation methods for coverage measurement conducted by [Li et al. \(2022\)](#) followed the methods of [Dethier et al. \(1993\)](#). We compared measurements made in July for analysis since this sampling period was consistent across the years studied. It also represents the time of maximum biomass and cover.

Light availability was measured using photosynthetically active radiation (PAR). A SunScan Canopy Analysis System was used to collect PAR values above plant canopy and 10 cm above the soil surface. The proportion of light penetrating the canopy was then calculated ([Li et al., 2022](#)). Initial measurements in March 2014 served as a baseline for pre-treatment. Four to five measurements per growing season were made during dosing while 1–2 were made during recovery. Analysis focused on comparing summer months (June and July), when aboveground biomass reaches its seasonal peak, except for 2017 when light was measured only in October.

## Appendix 6. SET and Elevation Methods

Rod SETs were installed in 2013 and allowed to equilibrate for 6 months before baseline measurements were made in January 2014 and before treatment were initiated in April 2014. Three arms of each SET protruded into the corresponding plot with each arm containing 9 pins to gather elevation measurements (i.e., 3 arms times 9 pins = 27 measurements per plot). SETs were measured twice a year (July, January) during dosing and recovery phases.

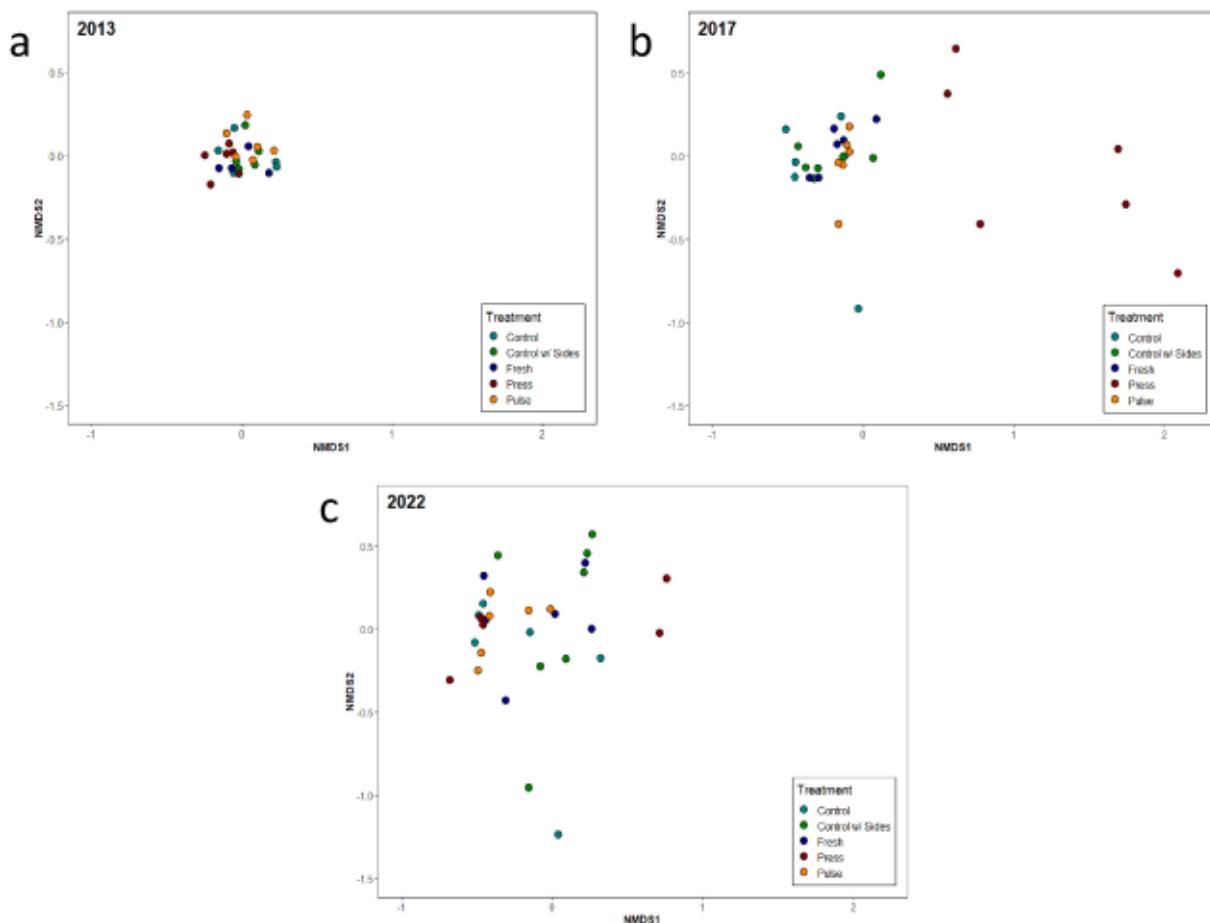
## Appendix 7. Porewater chemistry measurements during pre-dosing and the summer months of dosing and recovery from 2014 to 2020

Salinity						DRP					
Time	Treatments (ppt)					Time	Treatments ( $\mu\text{g-P/L}$ )				
	C	CS	F	Pr	Pu		C	CS	F	Pr	Pu
Pre (Jan 2014)	0.08	0.08	0.08	0.09	0.09	Pre (Jan 2014)	14	17.18	12.78	10.85	10.52
July 2014	0.5	0.05	0.04	3.35	0.06	July 2014	8.2 4	21.06	12.32	26.15	7.95
July 2017	0.08	0.07	0.05	0.96	0.08	July 2017	29. 16	30.23	29.78	168.5	100.68
Oct 2017	0.5	0.51	0.48	0.48	0.71	Oct 2017	17. 73	18.54	27.75	56.06	29.03
Post (Jun 2018)	0.05	0.04	0.04	0.1	0.06	Post (Jun 2018)	8.9 5	9.7	9/94	15.15	13.12
July 2019	0.03	0.03	0.04	0.15	0.1	July 2019	16. 13	19.78	19.24	39.17	28.57
Aug 2020	0.044	0.034	0.04	0.08	0.07	Aug 2020	8.6 12	8.125	9.362	5.77	16.36
Ammonium						Nitrate + Nitrite					
Time	Treatments ( $\mu\text{g-N/L}$ )					Time	Treatments ( $\mu\text{g-S/L}$ )				
	C	CS	F	Pr	Pu		C	CS	F	Pr	Pu
Pre (Jan 2014)	18.38	8.03	11.9	14.78	20.23	Pre (Jan 2014)	7.4 7	6.88	7.14	7.28	7.36
July 2014	5.45	5.68	6.33	47.83	4.46	July 2014	4.7 9	4.96	5.36	14.75	4.86
July 2017	13.87	9.73	8.84	366.83	16.52	July 2017	8.9 2	13.37	8.63	12.73	11.48
Oct 2017	26.87	17.26	17.64	153.65	20.62	Oct 2017	8.0 9	8.5	9.31	11.44	11.68
Post (Jun 2018)	6.53	9.45	6.94	28.9	12.73	Post (Jun 2018)	8.9 5	9.7	9.94	15.15	13.12
July 2019	12.42	8.65	7.96	14.83	6.37	July 2019	12. 3	20.23	12.96	11.38	11.58
Aug 2020	15.19	4.35	3.98	6.463	0.67	Aug 2020	7.9 6	6.82	8.33	13.23	9.39
Sulfide						DOC					
Time	Treatments ( $\mu\text{g-N/L}$ )					Time	Treatments (mg/L)				
	C	CS	F	Pr	Pu		C	CS	F	Pr	Pu
Pre (Jan 2014)	NA	NA	NA	NA	NA	Pre (Jan 2014)	10. 27	9.46	8.17	7.19	8.16
July 2014	0.15	0.52	0.18	14.71	0.77	July 2014	12. 47	11.12	11.2	9.91	11.96
July 2017	0.28	0.49	0.47	2.58	0.42	July 2017	11. 74	11.63	12.18	14.2	11.98
Oct 2017	0.22	0.42	0.46	0.67	0.97	Oct 2017	7.7 1	8.62	11.62	10.06	7.46
Post (Jun 2018)	0.24	0.69	0.51	0.3	0.56	Post (Jun 2018)	14. 74	15.36	14.94	16.66	14.76
July 2019	0.28	0.54	0.54	0.34	0.37	July 2019	12. 92	12.51	12.14	15.23	12.86
Aug 2020	0.18	0.23	0.41	0.21	0.26	Aug 2020	10. 3	10.03	9.32	11.21	9.97

**Appendix 8. Percentage of vegetation cover in July for dominant species during pre-dosing (2013) or initial dosing (2014), end of dosing (2017), one year into recovery (2018), and five years of recovery (2022)**

<i>L. repens</i>						<i>P. cordata</i>					
Time	Treatments (%)					Time	Treatments (%)				
	C	CS	F	Pr	Pu		C	CS	F	Pr	Pu
Pre (2013)	NA	NA	NA	NA	NA	Pre (2013)	29. 17	38.3 3	40	54.1 7	32.5
2014	71.6	98.3 3	73.3 3	0	83.3 3	2014	38. 33	30	50	18.3 3	35
2017	46.4	35	23.3 3	0.17	2.5	2017	31. 17	38.5 7	35	8	35
2018	5.17	1.43	2.67	8.33	0.67	2018	21. 67	22.8 6	21.6 7	15.5	14.1 7
Post (2022)	54.1	12.1	44.1 7	67.5	62.5	Post (2022)	39. 17	39.1 7	34.1 7	17.5	21.6 7
<i>P. hydropiperoides</i>						<i>Z. miliacea</i>					
Time	Treatments (%)					Time	Treatments (%)				
	C	CS	F	Pr	Pu		C	CS	F	Pr	Pu
Pre (2013)	95.8	100	97.5	90	96.6 7	Pre (2013)	75. 83	76.6 7	78.3 3	72.5	66.6 7
2014	96.6	98.3 3	91.6 7	10.8 3	93.3 3	2014	86. 67	88.3 3	86.6 7	70	83.3 3
2017	85.8 3	79.2 9	82.5	1	94.1 7	2017	76. 67	91.4 3	94.1 7	32.5	80
2018	58.3	45.7	45.7 1	2	68.3 3	2018	52. 5	67.8 6	61.6 7	15	48.3 3
Post (2022)	64.1	36.4	36.4 3	64.1	70.8 3	Post (2022)	70. 33	77.1 4	85	65	84.1 7

**Appendix 9. NMDS clustering of treatments based on plant community composition (a) before dosing (2013), (b) at the end of dosing (2017), and at the end of the recovery period (2022)**



**Appendix 10. Average percentage of light penetration before, during, and after dosing**

Time	Treatments (%)				
	C	CS	F	Pr	Pu
Pre (Mar 2014)	16.54	21.54	18.06	23.48	27.83
Jun-14	34.68	46.04	38.27	52.38	50.09
Oct-17	22.58	14.66	19.33	63.46	23.41
Jul-18	9.00	15.53	16.39	30.81	15.71
Post (Jul 2022)	12.14	17.28	20.52	23.59	24.12

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