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Experimental Saltwater Intrusion Drives Rapid Soil Elevation and Carbon Loss in Freshwater and Brackish Everglades Marshes

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Abstract

Increasing rates of sea-level rise (SLR) threaten to submerge coastal wetlands unless they increase soil elevation at similar pace, often by storing soil organic carbon (OC). Coastal wetlands face increasing salinity, marine-derived nutrients, and inundation depths from increasing rates of SLR. To quantify the effects of SLR on soil OC stocks and fluxes and elevation change, we conducted two mesocosm experiments using the foundation species sawgrass (*Cladium jamaicense*) and organic soils from freshwater and brackish Florida Everglades marshes for 1 year. In freshwater mesocosms, we compared ambient and elevated salinity (fresh, 9 ppt) and phosphorus (ambient, + 1 g P m^{-2} $year^{-1}$) treatments with a 2 × 2 factorial design. Salinity addition reduced root biomass (48%), driving 2.8 ± 0.3 cm $year^{-1}$ of elevation loss, while soil elevation was maintained in freshwater conditions. Added P increased root productivity (134%) but also increased breakdown rates (k) of roots (31%) and leaves (42%) with no effect on root biomass or soil elevation. In brackish mesocosms, we compared ambient and elevated salinity (10, 19 ppt) and inundated and exposed conditions (water level 5-cm below and 4-cm above soil). Elevated salinity decreased root productivity (70%) and root biomass (37%) and increased k in litter (33%) and surface roots (11%), whereas inundation decreased subsurface root k (10%). All brackish marshes lost elevation at similar rates (0.6 ± 0.2 cm $year^{-1}$). In conclusion, saltwater intrusion in freshwater and brackish wetlands may reduce net OC storage and increase vulnerability to SLR despite inundation or marine P supplies.

Keywords Saltwater intrusion · Carbon storage · Sea-level rise · Ecosystem vulnerability · Elevation change · Coastal wetlands · Phosphorus · Salinity · Inundation

Introduction

Coastal wetlands are highly efficient sinks for carbon dioxide and have among the highest organic carbon (OC) accumulation rates and soil carbon inventories of any ecosystem types (Chmura et al. 2003; Bouillon et al. 2008; McLeod et al. 2011). Peat soils in coastal wetlands develop slowly over centuries to millennia, as OC inputs from primary production outpace slow rates of organic matter decomposition in inundated soils, serving as C sinks that mitigate climate change (Griscom et al. 2017). Furthermore, particularly in coastal wetlands with organic soils, belowground biomass and soil OC are often the largest drivers of wetland elevation change (Nyman et al. 2006; McKee et al. 2007; Neubauer 2008; Brighthaupt et al. 2017), allowing many coastal wetlands to maintain elevation with gradual rates of sea-level rise (SLR) for millennia (Woodroffe 1990; McKee et al. 2007). Disturbances can enhance the decomposition of organic matter stocks held within soils, leading to high levels of CO_2

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emissions and elevation loss (Pendleton et al. 2012; Kauffman et al. 2017; Lovelock et al. 2017). In particular, as the rate of SLR accelerates (Nerem et al. 2018), many coastal wetlands are being exposed to saltwater intrusion and increasing inundation depth (Kirwan and Megonigal 2013; Herbert et al. 2015; Morris et al. 2016). Disturbances can alter the production and decomposition of organic matter stocks held within soils, leading to elevation change (Pendleton et al. 2012; Kauffman et al. 2017; Lovelock et al. 2017). However, as the rate of SLR accelerates (Nerem et al. 2018), many coastal wetlands are being exposed to higher salinities and inundation depths (Kirwan and Megonigal 2013; Herbert et al. 2015; Morris et al. 2016). The proportion of coastal wetlands likely to be submerged by SLR is largely dependent on biophysical feedbacks among soils, plants, and shifting environmental conditions (Kirwan et al. 2016).

Saltwater intrusion is particularly widespread and rapid in coastal wetlands that have anthropogenic reductions in freshwater flows (Ardón et al. 2016; Herbert et al. 2015; Trenberth et al. 2014; Dessu et al. 2018). The Florida Everglades is especially susceptible to rapid saltwater intrusion and increased inundation depths due to low elevation, extensive upstream freshwater diversion, and porous karstic bedrock (McVoy et al. 2011; Dessu et al. 2018). The majority of the Everglades is less than 1.5 m above sea level (Titus and Richman 2001). Thus, by the end of this century, upper estimates of 2–2.5 m of projected SLR (Sweet et al. 2017) are likely to drive widespread saltwater intrusion and increase depth and frequency of inundation through much of the ecosystem. Everglades freshwater marshes are generally P-limited, but the intrusion of saltwater enhances P availability (Sandoval et al. 2016) by providing marine-derived P (Childers et al. 2006), and by releasing P adsorbed to limestone bedrock (Price et al. 2010; Flower et al. 2017b). Freshwater flows to the Everglades have also been drastically reduced through the creation of 2500 km of canals (Sklar et al. 2005; McVoy et al. 2011), driving peat loss within the northern region of the Everglades (Hohner and Dreschel 2015). However, a large component of Everglades restoration focuses on enhancing freshwater flow to the southern Everglades to reduce rates of saltwater intrusion (Sklar et al. 2005). Models predict increased rates of saltwater intrusion and inundation depths in the Everglades, but large uncertainties exist based on rates of SLR, changes to precipitation, and freshwater management (Flower et al. 2017a).

In coastal peatlands with low sediment availability, the accumulation of OC from autochthonous organic matter, particularly roots, drives elevation change (Nyman et al. 1993; Nyman et al. 2006; Morris et al. 2016), but saltwater intrusion and increased inundation may alter OC stocks and inputs. Saltwater intrusion can alter OC inputs negatively by both introducing a stressor (salinity) and by increasing the depth and frequency of inundation and positively by introducing a resource (P), creating a trade-off in plant productivity and biomass allocation (Huston 1997; Krauss et al. 2009; Neubauer et al. 2013; Herbert et al. 2015). Salinity is negatively related to aboveground sawgrass productivity across the Everglades (Ewe et al. 2006; Macek and Rejmankova 2007; Troxler et al. 2014) and elsewhere in coastal wetlands of the southern USA (Macek and Rejmankova 2007; Wilson et al. 2015). However, the interaction of salinity and P availability creates a peak in aboveground productivity along the leading edge of saltwater intrusion, due to enhanced P availability (Ewe et al. 2006; Troxler et al. 2014). Much less is known about the interactions of salinity and P on belowground biomass and production. Plants alter their above-/belowground biomass partitioning based on available resources (Tilman 1985); therefore, as P becomes more available, plants may allocate a lower proportion of their biomass and production to roots, as what occurs in Everglades mangroves swamps (Castañeda-Moya et al. 2011). Finally, moderate inundation can increase plant productivity, but in excess, causes reduced plant productivity or mortality (Kirwan and Megonigal 2013; Troxler et al. 2014).

Changes in organic matter breakdown rates can alter OC accumulation and may be impacted by saltwater intrusion and inundation, but to date, results have been mixed. Saltwater intrusion creates a similar trade-off in microbial breakdown rates, as salinity can stress microbial communities and decrease breakdown rates (Neubauer et al. 2013; Servais et al. 2019), whereas nutrients and sulfate in saltwater can stimulate microbial breakdown of organic matter (Qualls and Richardson 2008; Weston et al. 2011; Woodward et al. 2012; Neubauer et al. 2013; Chambers et al. 2013, 2019). Finally, inundation can decrease OC breakdown by enhancing the development of reduced soil conditions (Ise et al. 2008), but other studies have found evidence of enhanced breakdown with greater inundation (Kirwan et al. 2013).

Rapid saltwater intrusion in the Everglades has coincided with an expansion of both areas with sparse vegetation and of open water ponds (Ross et al. 2000; Chambers et al. 2015), suggesting OC loss. Loss of vegetated coastal marsh can occur when the rate of wetland elevation gain is lower than the rate of SLR (Kirwan and Megonigal 2013). In organic wetland soils, some wetlands experience rapid elevation loss that converts vegetated wetlands to open ponds, driven by a net loss in soil OC, which in turn is caused by enhanced decomposition and loss of soil structure from root death (Delaune et al. 1994; Cahoon et al. 2003; Deegan et al. 2012). Due to their location in the landscape and the disruption of biophysical feedbacks that drive elevation gain, brackish marshes are most at risk of increasing inundation depths (Flower et al. 2017a). Peat collapse in the Everglades coincides with saltwater intrusion (Wilson et al. 2018), but the specific cause is not fully understood (Chambers et al. 2015, 2019).

Much of the uncertainty over coastal wetland vulnerability to SLR concerns the degree to which biophysical feedbacks will enhance or diminish soil OC storage and vertical elevation gain as environmental conditions change (Kirwan et al. 2016). In addition, saltwater intrusion rates are highly variable across the landscape due to the influence of topography (elevation), tidal exposure, underlying geology, and connectivity to freshwater (Ross et al. 2000; Price et al. 2010; Flower et al. 2017a). To better understand impacts of saltwater intrusion, it is important to quantify the likely changes in salinity, nutrient availability, and inundation, both independently and in combination.

We used mesocosm experiments to quantify the impacts of salinity, P availability, and inundation on OC stocks and fluxes and soil elevation change in freshwater and brackish marshes. To simulate initial saltwater intrusion in freshwater marsh mesocosms, we quantified the responses of OC stocks and fluxes to ambient (fresh) and elevated salinity (~ 9 ppt) and ambient and elevated P loading. In brackish marsh mesocosms, we compared ambient (~ 10 ppt) and elevated (~ 19 ppt) salinity levels and different inundation regimes (5 cm below the soil surface or 4 cm above the soil surface) to simulate shifting hydrologic conditions. We predicted that (1) salinity would decrease OC storage and soil elevation by decreasing root productivity and biomass and increasing organic matter breakdown; (2) salinity would have a stronger effect on OC storage in brackish than freshwater marshes because of moderate salinity tolerance in sawgrass; (3) P would interact with salinity additions to mitigate salt stress on root productivity but synergistically enhance breakdown, causing soil elevation loss compared to ambient freshwater; and (4) inundation would reduce organic matter breakdown and root ingrowth with no effect on soil elevation.

Methods

Experimental Design

Freshwater Marsh Mesocosms

We collected 24 plant-peat monoliths (30 cm deep × 30 cm wide × 40 cm long) from a nontidal, freshwater peatland in the Florida Everglades (25° 46′ 06.1″ N, 80° 28′ 56.2″ W), dominated by a dense stand of *Cladium jamaicense* Crantz (sawgrass). The phosphorus load in this area is comparable to or lower than P loading into Everglades National Park and is not nutrient enriched (Wilson et al. 2018; Servais et al. 2019; Xue 2018). After excavation, plant–soil monoliths were placed in mesh lined plastic bins and transported to an outdoor mesocosm facility at the Florida Bay Interagency Science Center in Key Largo, FL. Plant soil monoliths were placed in polycarbonate boxes and randomly assigned to one of four treatments. We maintained water levels ~ 1 cm above the soil surface and conducted a 2 × 2 factorial design with two factors (salinity and P). Our design created four treatments, each with six monoliths to represent freshwater [Fresh], elevated salinity [Salt], freshwater and elevated P [Fresh + P], and elevated salinity and P [Salt + P]).

We targeted a salinity treatment of ~ 9 ppt because this was the ambient porewater salinity at a historically freshwater field site where we have witnessed recent peat collapse (Wilson et al. 2018). We maintained salinity by collecting local fresh and saltwater from nearby ecosystems, storing water in 7750-l head tanks and mixing to desired salinity concentration and adding to mesocosms 2–3 times per week. Freshwater was collected from a nearby canal (C-111 canal; 25° 17′ 31.74″ N, 80° 27′ 21.59″ W) with similar nutrient concentrations to freshwater marshes of the Everglades. Saltwater head tanks drew water from the adjacent Florida Bay. Notably, fresh and saltwater sources had similar nutrient and sulfate concentrations and only differed significantly in salinity content (Servais et al. 2019). In total, we added 22 kg m^{-2} year^{-1} of salt to each salt-treated sawgrass-peat monolith (Salt and Salt + P). Source water was mixed to the appropriate salinity before addition to ensure homogeneous delivery. For our P treatment, we added 1 g m^{-2} year^{-1} P continuously as 2.25 mg L^{-1} diluted phosphoric acid at 0.14 mL min^{-1} to each P-treated sawgrass peat monolith over the course of the experiment. Total P loads were calculated for each monolith based on cumulative added P and the added P from source waters (based on molar P concentrations and volume of source water added). Because the Everglades is P limited, most added P is quickly taken up by biota and therefore can be undetected in surface waters, making P loads difficult to quantify across the landscape. We chose our P loading rate to elicit a low-level response based on other experimental and field results (Craft et al. 1995; Gaiser et al. 2005; Macek and Rejmankova 2007; Wilson et al. 2018). We measured salinity (ppt) monthly in surface and porewater using a YSI Model 600 XL (Xylem, Inc., Yellow Springs, OH, USA). Samples of added water were stored at − 20 °C until analyzed at the Southeast Environmental Research Center Nutrient Analysis Laboratory at Florida International University. Total added P was analyzed on an Alpkem RFA 300 autoanalyzer (OI Analytical, College Station, TX, USA).

Brackish Marsh Mesocosms

We extracted 24 plant–soil monoliths (30-cm diameter × 30-cm depth) from a brackish, sawgrass-dominated marsh with peat soil within Shark River Slough in Everglades National Park (25° 13′ 13.5″ N, 80° 50′ 36.7″ W). Plant–soil monoliths were extracted intact on January 7, 2015, from a marsh that was freshwater in the 1950s (Wilson et al. 2018), but has experienced saltwater intrusion in ensuing decades, and had ~ 9 ppt ambient porewater salinity at the time of collection. Monoliths were extracted from peat soils (~ 1 m deep), above limestone bedrock. We exposed 24 brackish sawgrass-peat monoliths to a 2 × 2 factorial design altering salinity from ambient (9.7 ± 0.2 ppt) to elevated (18.9 ± 0.5 ppt) salinity and altering inundation from exposed (soil surface 4 cm above water level) to submerged (soil surface 5 cm below water surface). Our experimental design created four treatments: (1) Amb.Sub, (2) Amb.Exp, (3) Salt.Sub, and (4) Salt.Exp, where the salinity treatment was either ambient (Amb) or elevated (Salt) and the inundation treatment was either submerged (Sub) or exposed (Exp). Monoliths were placed in perforated, mesh-lined bins that allowed water flow, but contained soil. Monoliths were then immersed in six 250-gal concrete tanks, each equipped with an adjustable in-flow spigot and a 30-cm standpipe with an outflow drain to maintain consistent water level. We mixed salt and freshwater from the head tanks mentioned above on a weekly basis, and the mixture was pumped at a constant flow (36 mL min^{-1}) through the flow-through system. Each tank was either supplied with elevated or ambient salinity water, while inundation level was controlled by either placing monoliths on the tank bottom to create inundated conditions, or on a shelf that exposed the soil surface. For the brackish marsh experiment, we used a flow-through experiment, because there was no risk of cross-contamination from adjacent plots since only the salinity treatment altered water chemistry.

Root Biomass and Productivity

We measured root productivity in all plant–soil monoliths and both experiments through the ingrowth method (Vogt et al. 1998), using cylindrical mesh bags (2.5-cm diameter, 15-cm depth) filled with commercial peat moss. We incubated root ingrowth cores for 6-month intervals over the experiment and summed the two intervals to determine total productivity over 1 year. In addition, we measured final belowground root biomass from soil cores (2.5-cm diameter × 25-cm depth) at the end of the experiment to determine shifts in root biomass stocks. Root cores were sieved through 1-mm mesh sieves. Live roots were identified based on color, texture, and pliability and collected for biomass measurements.

We kept all organic matter samples (live and decomposing roots and leaf litter) on ice until processing, rinsed them of sediment with deionized water, dried them at 40 °C until mass stabilized, and weighed them for mass. Dried samples were ground using an 8000-D ball mill (Spex SamplePrep, Metuchen, NJ, USA), and proportion organic matter was calculated from ash free dry mass (AFDM) as loss on ignition in a muffle furnace at 550 °C for 5.5 h. We calculated OC as 50% of organic mass (Karam 1993).

In the freshwater mesocosm experiment, we also measured nutrient content and molar ratios in root and leaf samples. We measured total C and total nitrogen (N) content using a Carlo Erba NA 1500 CHN Analyzer (Carlo Erba, Milan, Italy) (Zimmermann and Keefe 1997). We measured total phosphorus (P) content using the ash/acid extraction method followed by spectrophotometric analysis run on a UV-2 spectrophotometer (Shimadzu Corp., Kyoto, Japan) (Solorzano and Sharp 1980). We calculated elemental ratios (C:N, C:P, N:P) as molar mass.

Organic Matter Breakdown Rates

In the freshwater mesocosms, we incubated oven-dried (40 °C) sawgrass leaf litter for 80, 166, 267, and 361 days in 1-mm mesh litterbags (beginning 24 February 2015). Oven-dried (40 °C) root litter was incubated at 0–7.5 and 7.5–15 cm depths for 361 days. All organic matter breakdown samples were kept on ice until processing. Organic matter samples were rinsed of sediment with deionized water, dried at 40 °C until mass stabilized, and weighed for mass remaining. We express organic matter breakdown as proportion of AFDM remaining over 1 year. We estimated breakdown rate, k, using a negative exponential decay model based on the fraction of AFDM remaining vs. time (Benfield 2006). The specific model used is $M_t = M_0 \times e^{-kt}$, where M_0 is the initial litter mass, M_t is the litter mass on a given sampling day, and t is time (days of incubation).

In brackish mesocosms, senescent sawgrass leaf litter was similarly deployed, but due to restricted soil surface area in the brackish experiment, we were only able to determine breakdown after 361 days. As in freshwater treatments, root k values were determined after 361 days. All litter and root k values were calculated from mass loss from AFDM.

Soil Elevation Change

Soil elevation change was measured from fixed benchmarks to the soil surface after 65, 166, 265, and 361 days exposure to elevated salinity and phosphorus (freshwater mesocosms) and elevated salinity and inundation (brackish mesocosms). We standardized elevation measurements by establishing two fixed locations (10 cm north and south of the center of each soil monolith) within each experimental mesocosm to measure elevation change. Our mesocosms were located within concrete tanks, which we used as a permanent benchmark above the soil surface and measured distance from crypt edge down to the soil surface. The rate of change was measured as difference from baseline and standardized to represent change in centimeters per year.

Data Analyses

We used a two-way analysis of variance (ANOVA) to determine the impact and interaction of our treatments on the freshwater mesocosm experiment (salinity, phosphorus, and their interaction) and in the brackish mesocosm experiment (salinity, inundation and their interaction; alpha level of 0.05). Where significant differences among response variables were identified, Tukey's HSD post hoc comparison was used to determine the differences among the four treatment types in the freshwater and brackish mesocosm experiments. All analyses were performed using R (version 3.3.2, R Core Team 2016). All results were presented as percent difference between means of significantly different treatments.

Results

Experimental Treatments

In freshwater mesocosms, porewater salinity was higher in our salinity treatments (8.8 ± 0.18 ppt) compared to fresh treatments (0.45 ± 0.01 ppt). Similarly, we increased porewater soluble reactive phosphorus from 0.17 ± 0.03 μmol L^{-1} in treatments without added P to 0.39 ± 0.02 μmol L^{-1} in treatments with added P.

In brackish mesocosms, porewater salinity was higher in added salinity treatments (18.9 ± 0.5 ppt) compared to ambient conditions (9.7 ± 0.2 ppt). Consistent with our experimental design, we maintained inundation at either exposed (soil surface 4 cm above water level) or inundated (soil surface 5 cm below water level) conditions.

Impacts of Salinity and Phosphorus on Freshwater Mesocosms

Root Biomass and Productivity

In freshwater mesocosms, P additions increased root productivity 134% ($P = 0.004$; Table 1). Salinity did not impact root productivity ($P > 0.05$). Among our four treatments, root productivity was higher in the Fresh + P than the Salt treatment ($P = 0.02$); otherwise, treatments were similar ($P > 0.05$; Table 1). Added P did not impact root biomass ($P > 0.05$). Salinity addition decreased final root biomass by 48% ($P = 0.03$; Table 1). There were no significant differences in root biomass among our four treatment groups ($P > 0.05$; Table 1).

Organic Matter Breakdown

In freshwater mesocosms, P additions increased the rate of root breakdown by 33% in soil at 0–7.5 cm belowground ($P < 0.001$; Table 1) and 29% in deeper soil (7.5–15 cm) (Servais et al. 2019; $P = 0.007$; Table 1). Salinity had no impact on root breakdown in freshwater mesocosms ($P > 0.05$). Among our four treatments, surface root breakdown was faster in the Salt + P treatment than either treatment without added P (Fresh and Salt) ($P < 0.05$), but was similar to the Fresh + P treatment (Table 1). Among our treatments, deeper roots broke down faster in the Fresh + P treatment than any other treatment ($P < 0.05$; Table 1).

In freshwater mesocosms, P increased the rate of leaf litter breakdown on the soil surface 20% after 361 days ($P < 0.001$; Table 1). Among our four treatments, Fresh + P and Salt + P broke down faster than the Fresh and Salt treatments ($P < 0.001$; Table 1).

Sawgrass leaf litter mass loss was greater in added phosphorus (Fresh + P and Salt + P) treatments than ambient phosphorus (Fresh and Salt) treatments from 267 days to the end of the experiment (Fig. 1a). Litter mass loss was similar among treatments after 65 days of treatment. After 166 days, the Fresh + P treatment broke down faster than the Fresh treatment, while other treatments were similar. Leaf litter breakdown rate followed an exponential curve overall, but treatments with added P continued to breakdown at similar rates throughout the 361 days, while breakdown rates in treatments with ambient decreased with time (Fig. 1a).

Table 1 Soil OC change in response to salinity and phosphorus addition in a freshwater marsh mesocosm experiment

	Freshwater marsh mean (SE)				Significant effects	*P* values
	Fresh	Fresh + P	Salt	Salt + P		
Root productivity (g OC m^{-2} year^{-1})	81.34 (13.41)^{ab}	179.28 (37.3)^{a}	49.07 (13.77)^{b}	126.53 (33.43)^{ab}	P (+)	0.004
Root biomass (g OC m^{-2})	456 (147.4)	599.1 (121.8)	252.4 (65.7)	301.2 (57.5)	Salinity (−)	0.03
Leaf litter k day^{-1}	0.0014 (0.0001)^{a}	0.002 (0.0001)^{b}	0.0015 (0.0001)^{a}	0.002 (0.0002)^{b}	P (+)	< 0.001
Root k day^{-1} (0–7.5 cm)	0.00086 (0.00008)^{a}	0.00108 (0.00005)^{ab}	0.00083 (0.00004)^{a}	0.00117 (0.0001)^{b}	P (+)	0.002
Root k day^{-1} (7.5–15 cm)	0.00083 (0.00009)^{a}	0.00117 (0.00008)^{b}	0.00072 (0.00003)^{a}	0.00083 (0.00008)^{a}	P (+)	0.007
Elevation change (cm year^{-1})	− 0.04 (0.83)^{ab}	0.88 (0.63)^{a}	− 2.75 (0.51)^{b}	− 2.29 (0.38)^{b}	Salinity (−)	< 0.001

Mean and standard error for each treatment type ($n = 6$ per treatment). The driver and direction of effects and significant P values ($P < 0.05$) from two-way ANOVAs are included, and $P > 0.05$ is reported as NS (not significant). Superscripted letters represent results from Tukey's HSD test performed among our four individual treatments. If no letters are present, there were no significant differences between treatments. Root breakdown rates were previously reported in Servais et al. (2019)

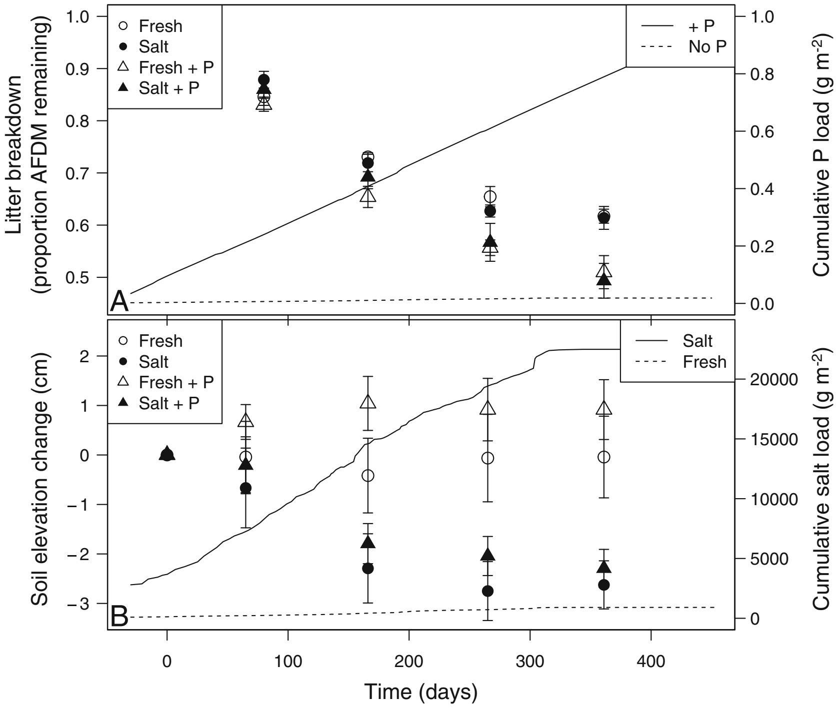

Fig. 1 Litter breakdown and elevation change through time in freshwater marsh mesocosms. **a** There was no difference in proportion leaf litter ash free dry mass (AFDM) remaining after 80 days, but Fresh + P and Fresh became significantly different after 166 days, and all P treatments broke down faster after 267 and 361 days ($P < 0.01$). **b** Salinity decreased soil elevation over the course of 361 days. Salinity caused a rapid elevation loss after 166 days ($P < 0.05$), after which elevations remained similar ($P > 0.05$)

Elevation Change

In freshwater mesocosms, added salinity (Salt) drove soil elevation loss of 2.8 ± 0.5 cm year^{-1} ($P < 0.001$) as compared with 2.3 ± 0.4 cm in the Salt + P treatment (Fig. 1b; Table 1). Soils in Salt and Salt + P treatments lost more elevation than those in the Fresh + P treatment ($P < 0.05$), whereas soils in the Fresh treatment had similar elevation and were not different from other treatments ($P > 0.05$; Table 1). Finally, a simple linear model showed that final root biomass was positively related to elevation change ($R^2 = 0.3$; $P = 0.003$), where elevation loss was linked to low root biomass.

Salinity treatments drove a rapid decrease in elevation between 0 and 166 days, creating a significant loss in elevation from both initial elevation and freshwater treatments ($P < 0.05$) (Fig. 1b; Table 1). However, there was no significant change in elevation after the rapid initial shift ($P > 0.05$; Fig. 1b). To maintain our saltwater treatment, we loaded salinity until 270 days, but once salinity stabilized, elevation remained constant as well (Fig. 1b).

Root and Leaf Litter Stoichiometry

Roots from our root productivity measurements in the freshwater mesocosm experiment had similar nutrient concentrations (%C, %N, %P) and nutrient ratios in all treatments ($P > 0.05$; Table 3). Similarly, there was no difference in nutrient concentrations or nutrient ratios in living sawgrass leaves ($P > 0.05$; Table 3).

After incubating decomposing leaf litter for 1 year, P concentration was 309% higher in the added P treatments than ambient P treatments, driving decreases in C:P (− 67%) and N:P (− 70%) ratios ($P < 0.001$; Table 3). Nutrient content of roots was not impacted by P additions; however, in decomposing roots, P addition decreased N:P in the 0–7.5-cm depth profile ($P = 0.006$) but did not impact C:N or C:P ratios ($P > 0.05$). P addition did not impact nutrient ratios in deeper soil ($P > 0.05$; Table 3).

Salinity drove a consistent decrease in C concentration of decomposing organic matter. Salinity decreased C content by about 3% in leaf litter on the soil surface and both root depths ($P < 0.05$; Table 3).

Impacts of Salinity and Inundation on Brackish Mesocosms

Root Productivity and Biomass

In brackish mesocosms, increased salinity decreased root productivity 70% ($P = 0.002$), but inundation did not alter root productivity ($P > 0.05$; Table 2). Among our four treatments, there were no significant differences ($P > 0.05$: Table 2). Additionally, salinity decreased living root biomass 37% ($P = 0.02$; Table 2), while inundation had no effect ($P > 0.05$). Among our four treatments, there were no significant differences ($P > 0.05$: Table 2).

Table 2 Soil OC change in response to salinity addition and increased inundation in brackish marsh mesocosms

	Brackish marsh mean (SE)				Significant effects	P values
	Ambient exposed	Ambient submerged	Salt exposed	Salt submerged		
Root productivity (g OC m^{-2} year^{-1})	67.8 (10.2)^{a}	69.6 (18.7)^{a}	21.0 (8.9)^{b}	20.2 (5.6)^{b}	Salinity (−)	0.02
Root biomass (g OC m^{-2})	122.1 (17.1)	128.1 (13.3)	84.1 (19.1)	73.0 (8.1)	Salinity (−)	0.03
Leaf litter k day^{-1}	0.0024 (0.0003)	0.0013 (0.0002)	0.002 (0.0002)	0.002 (0.0003)	Salinity (+)	0.05
Root k day^{-1} (0–7.5 cm)	0.00077 (0.00003)^{a}	0.00074 (0.00002)^{a}	0.00088 (0.00004)^{b}	0.00079 (0.00003)^{ab}	Salinity (+)	0.02
Root k day^{-1} (7.5–15 cm)	0.00091 (0.00002)	0.00083 (0.00004)	0.00096 (0.00003)	0.00084 (0.00004)	Inundation (−)	0.03
Elevation change (cm year^{-1})	− 0.46 (0.28)	− 0.75 (0.22)	− 1.29 (0.24)	− 0.58 (0.26)	NS	

Mean and standard error for each treatment type ($n = 6$ per treatment). The driver and direction of effects and significant P values ($P < 0.05$) from two-way ANOVAs are included, and $P > 0.05$ is reported as NS (not significant). Superscripted letters represent results from Tukey's HSD test performed among our four individual treatments. If no letters are present, there were no significant differences between treatments

Organic Matter Breakdown Rates

In brackish mesocosms, salinity increased root k 11% at 0–7.5 cm ($P = 0.02$; Table 2). In deeper soil (7.5–15 cm), inundation decreased root breakdown 4% ($P = 0.03$; Table 2). There were no significant differences among our four treatments ($P > 0.05$; Table 2).

In brackish mesocosms, added salinity increased leaf litter k on the soil surface by 33%, but inundation did not have an impact ($P > 0.05$; Table 2). There were also no differences in k among treatments ($P > 0.05$; Table 2).

Soil Elevation Change

In brackish mesocosms, neither salinity nor inundation treatments had a significant impact on elevation change ($P > 0.05$). However, all treatments lost elevation over the course of the experiment ($P = 0.007$, mean = 0.77 cm year^{-1} loss; Table 2).

Discussion

Our results demonstrate that salinity from saltwater intrusion into coastal peat marshes can drive a decrease in OC storage and loss of soil elevation. We found that freshwater marshes responded to a moderate increase in salinity (0 to 9 ppt) with rapid soil elevation loss (2.8 cm in 1 year), which was directly related to a decrease in root biomass ($R^2 = 0.3$; $P = 0.03$). We found that the subsidy of P associated with saltwater intrusion increased root productivity, but also increased root breakdown and therefore did not impact soil elevation. Furthermore, increased salinity in brackish marshes (10 to 19 ppt) continued to reduce OC storage by decreasing root biomass and productivity and increasing root breakdown. Although we did not find a difference in elevation change among brackish treatments, we found a reduction in OC inputs and an increase in OC loss that is likely to reduce OC storage and elevation change over time. Furthermore, in both experiments, salinity treatments with 9 ppt or greater lost elevation, whereas freshwater treatments maintained elevation, indicating that saltwater intrusion is likely to have a negative impact on elevation through time. Below we examine the impacts of salinity, P, and inundation on OC storage and elevation change in Everglades coastal peat wetlands and consider the implications of accelerating SLR and freshwater management on ecosystem vulnerability in coastal wetlands more broadly.

Salinity as a Plant Stressor

Elevated salinity had a strong negative influence on wetland OC storage by reducing plant root biomass and productivity. In freshwater marsh mesocosms, increasing salinity from 0 to 9 ppt decreased living root biomass by half and created a trend toward reduced root ingrowth ($P > 0.05$). Whereas other species of coastal marsh plants may be killed by increasing salinity from 0 to 9 ppt, sawgrass has a wide salinity tolerance dominating freshwater marshes and existing at average salinities up to 16.4 ppt (Troxler et al. 2014). However, salinity often causes reduced productivity at sublethal levels. For instance, Macek and Rejmankova (2007) found reduced above- and belowground sawgrass biomass when salinity was raised from 0 to 5 ppt, whereas Wilson et al. (2015) found decreased productivity at 4.7 ppt compared to 2.3 ppt. In brackish marsh mesocosms, we found continued loss in root biomass (− 37%) and productivity (− 70%) when we increased salinity from 10 to 19 ppt. Our experimental manipulation (19 ppt) exceeds the average yearly salinity levels that sawgrass tolerates but falls well below the maximum short-term (30 days) salinity that they survive (Troxler et al. 2014). Because of the dynamic nature of the Everglades ecotone, the best predictor of sawgrass aboveground productivity in marshes has been shown to be the number of days salinity exceeds 30 ppt (Troxler et al. 2014). Our results show that sawgrass is negatively impacted by salinity intrusion in both freshwater and brackish marsh, but that the impact was greater at higher salinity. However, in this habitat, the loss of soil OC in sawgrass marshes may be more extensive belowground because sawgrass marshes experience root mortality and reduced productivity.

Salinity did not impact root breakdown rates in our freshwater experiment but enhanced breakdown of leaf litter (33%) and shallow roots (11%) in the brackish experiment, which illustrates trade-offs in subsidies and stressors provided by saltwater. Salinity creates osmotic stress for freshwater-adapted microbes and can reduce organic matter breakdown (Neubauer et al. 2013) but also provides sulfate as an alternative electron acceptor (Weston et al. 2011; Neubauer et al. 2013; Chambers et al. 2013). Salinity probably had no impact on breakdown rates in our freshwater experiment because we focused on the established freshwater microbial community, which demonstrated a decrease in microbial biomass and enzyme activity (Servais et al. 2019), whereas brackish sawgrass marshes in the Everglades experience large seasonal swings in salinity (Troxler et al. 2014) and, therefore, likely had a salt-adapted microbial community, capable of withstanding salinity stress and taking advantage of additional sulfate subsidies. We only measured root breakdown rates to 15 cm and suspect that in deeper more reduced soils, saltwater (and associated sulfate) may have a greater effect on breakdown rates.

Our results suggest that salinity additions can decrease root biomass and soil elevation in freshwater wetlands and drive a net loss of OC in brackish marshes by reducing root stocks and productivity and increasing the breakdown of organic carbon.

Phosphorus as a Subsidy for Plant Productivity and Organic Matter Breakdown

Phosphorus addition increased root productivity by 134%, mirroring field data that shows an increase in productivity along the leading edge of saltwater intrusion (Ewe et al. 2006; Troxler et al. 2014). Saltwater intrusion has driven an increase in P availability throughout the coastal Everglades (Sandoval et al. 2016) because P is more available in seawater than freshwater (Childers et al. 2006), and, as saltwater intrudes into freshwater marshes, P adsorbed to limestone bedrock is rapidly released, providing a pulse of P (Price et al. 2010; Flower et al. 2017b). In addition, freshwater from the Everglades interior often carries anthropogenic P, which has enhanced P availability in parts of the freshwater Everglades (Qualls and Richardson 2008). Roots are frequently the most important long-term OC source to wetlands due to their recalcitrant nature and deposition in low-oxygen wetland soils (Mitch and Gosselink 2007; McKee et al. 2007; Deegan et al. 2012). In our study, P increased root productivity, a major component of OC storage and elevation gain, and doubled both aboveground biomass and aboveground net primary productivity (Wilson et al. 2018).

Phosphorus additions in our study also increased OC loss by enhancing leaf litter (33%) and root breakdown rates (42%), counteracting the influence of increasing OC inputs from primary productivity. A number of studies have shown increased breakdown rates associated with P additions to Everglades litter (Qualls and Richardson 2000; Qualls and Richardson 2008) and peat soils (Newman et al. 2001; Qualls and Richardson 2008) because heterotrophic microbes use available P to consume organic matter with C:P ratios too high to build microbial biomass (Swift et al. 1979). Because there is much more OC stored as soil organic matter than biomass, the stimulation of organic matter breakdown rates is critically important to quantifying climate change feedbacks (Scharlemann et al. 2014).

Two key drivers of organic breakdown rates in ecosystems are organic matter stoichiometry (Cornwell et al. 2008) and the availability of nutrients in the ecosystem. In our study, P addition led to greater P concentration and altered nutrient ratios in decomposing leaf litter on the soil surface, but did not change P concentration in living roots or leaves, indicating that P was rapidly scavenged by microbes to enhance organic matter breakdown, but is unlikely to change the quality of organic matter being produced. P was rapidly scavenged by microbes at the soil surface and decreased with depth, where concentrations in decomposing litter on the soil surface were 3 times higher in added P treatments, whereas reduced N:P ratios showed signs of microbial P use on roots from 0 to 7.5 cm, and there was no difference in deeper roots. Although neither living root nutrient concentrations or ratios changed with P addition, root productivity increased 134% and aboveground net primary productivity doubled (Wilson et al. 2019), indicating that some added P was used to enhance plant productivity, and was stored in leaf litter and sequestered in recalcitrant root biomass. In our experiment, P was delivered to the water column, where it first came into contact with the soil surface, but saltwater intrusion in the Everglades also seeps through porous limestone and is delivered from below (Price et al. 2006), with potentially different consequences. In deep peat, saltwater intrusion is likely to enhance P availability below the root zone, where microbes, but not plants, will receive a P subsidy, enhancing breakdown without a concurrent increase in productivity, therefore causing OC loss. We found that P accumulated in P-treated bulk soil from the 7.5–15-cm depth profile after 1 year, but not in shallower soil, indicating that roots were capable of assimilating P near the surface, whereas soil microbes used more P in deeper soil (Servais et al. 2019). Our results suggest that P subsidies increase both root productivity and the breakdown of organic matter. Because of the counteracting influence of the enhancement of both soil OC inputs and losses, P did not create an overall change in soil elevation in our study.

Inundation as a Soil Stabilizer

Our results showed that 1 year of increased inundation at + 4 cm above the soil surface had a small positive net effect on OC storage because of reduced root breakdown and no impact on belowground productivity (Table 3). Increased inundation has been shown to increase accretion rates in tidal salt marshes because allochthonous sediment is only deposited during inundated conditions (Morris et al. 2002). Similarly, moderate increases in inundation can increase OC storage but can stress or kill plants above certain levels (Kirwan and Megonigal 2013). In Everglades marshes removed from the coastline, the concentration of suspended solids is low, and allochthonous sediment generally plays a limited role, with elevation change primarily driven by organic matter storage (Craft and Richardson 1993). Furthermore, the breakdown of soil OC is enhanced in oxidized conditions (Ise et al. 2008). Although our treatments were not made to simulate drought conditions, more extreme drying events can lead to the loss of soil OC and elevation (Wilson et al. 2018). Finally, soil water can play a direct role in soil elevation by influencing soil volume (Whelan et al. 2005; Rogers and Saintilan 2008). Thus, increased inundation in marshes will likely preserve OC and reduce marsh vulnerability to collapse.

Saltwater Intrusion and Soil Elevation Change

In nontidal peat marshes, the balance between inputs of organic matter (primarily as root biomass) and losses (breakdown of organic matter) largely determines soil elevation change (Baustian et al. 2012). Our results show that saltwater intrusion into coastal sawgrass marshes can drive the rapid loss of soil elevation in freshwater marshes, making them vulnerable to “peat collapse.” Wetland vulnerability to SLR is mostly assessed in salt marshes directly along the coast; however, we identified biophysical feedbacks that increase freshwater and brackish marsh vulnerability kilometers inland. In our freshwater marsh, a 48% decrease in living root biomass was the key driver that led to 2.8 cm of elevation loss over the course of 1 year, with 2 cm elevation loss occurring within 165 days (Fig. 1b). This loss of living roots and a decrease in elevation occurred despite no change in CO_2 uptake and aboveground productivity with elevated salinity (Wilson et al. 2018). Increasing salinity from freshwater to 9 ppt for 6 months caused a classic case of “peat collapse,” in which roots die from salinity stress, lose their turgor, and cause a rapid decrease in soil volume and decrease in soil elevation (Delaune et al. 1994; Chambers et al. 2019). In addition, the loss of roots impacts soil integrity by decreasing the structure provided by roots allowing soil OC to be eroded or lost to the water column. In our freshwater mesocosms, TOC in the water column increased 220% with added salinity, indicating a substantial OC loss from the soil (Servais et al. 2019), which has also been seen when increasing salinity in mangrove peat soils (Chambers et al. 2013). After 165 days of continuously elevated salinity, elevation changes normalized and did not change significantly over the remaining 6 months of the experiment (Table 2), suggesting that the most severe impacts of saltwater intrusion occurred upon initial exposure, as root biomass decreases, causing a large flux of soil OC into the water column.

Although roots in brackish marshes are sensitive to elevated salinity, we did not detect salt treatment effects on declining soil elevation. Brackish marshes lost 0.8 cm of soil elevation over the course of 1 year; however, elevated salinity did not impact loss rates. Elevated salinity in freshwater marsh experiments drove a greater proportional and total decrease in belowground biomass than elevated salinity in brackish marsh experiments. In addition, added salinity reduced root productivity and increased root breakdown but did not influence soil elevation loss in brackish marsh mesocosms. The likely reason salinity did not cause increased elevation loss in our brackish experiment is that peat-soil monoliths were collected from a brackish marsh that had likely already experienced root loss. Freshwater experiments experienced greater proportion loss of belowground biomass when exposed to enhanced salinity (48% decrease in freshwater versus 37% in brackish marsh) and brackish marshes had less living root biomass to lose (freshwater marshes had 400% greater belowground biomass than brackish marsh under ambient salinity conditions). Therefore, although we documented significant loss of belowground biomass in both experiments, the total decrease in root biomass in the freshwater experiment was 250 g m^{-2}, whereas in brackish marsh, salinity addition only decreased belowground biomass by 47 g m^{-2}. The larger loss of root biomass likely contributed to greater elevation loss in freshwater mesocosm experiments.

Added P had no impact on soil elevation in freshwater marsh mesocosms, because P enhanced both OC inputs from plant productivity and losses from breakdown. In the same experiment, our P subsidy drove a significant increase in CO_2 uptake and sequestration (Wilson et al. 2019), but this gain was mostly in aboveground biomass. Along the leading edge of saltwater intrusion, aboveground biomass is stimulated by P availability (Troxler et al. 2014), but our results suggest that this is unlikely to substantially enhance belowground biomass, or soil elevation. P addition to freshwater marsh has had mixed net impacts on OC storage in the Everglades. Craft and Richardson (1993) found that enhanced OC inputs outweighed enhanced breakdown, driving 50% higher OC accretion in P-enriched Everglades peat marshes (0.53 g m^{-2} $year^{-1}$). However, in the highly P-enriched Everglades agricultural area, decomposition has driven losses in soil elevation at rates as high as 3 cm per year, particularly after draining wetland soils for agriculture (Volk 1973; Tate 1980). It is important to note that because our study quantified changes over the course of 1 year, our

Table 3 Decomposing organic matter stoichiometry in freshwater marsh mesocosms ($n = 6$ per treatment) after 361 days

	Fresh	Fresh + P	Salt	Salt + P	Significant effects	*P* values
Leaf litter						
%N	0.88 (0.04)	0.81 (0.04)	0.81 (0.03)	0.72 (0.06)	NS	
%C	43.82 (0.30)^{ab}	44.48 (0.12)^{a}	42.91 (0.58)^{bc}	42.42 (0.19)^{c}	Salinity (−)	< 0.001
%P	0.05 (0.004)^{a}	0.16 (0.031)^{b}	0.05 (0.005)^{a}	0.17 (0.03)^{b}	P (+)	< 0.001
C:N	58 (3)	65 (3)	62 (2)	71 (5)	P (+)	0.037
C:P	2248 (156)^{a}	838 (123)^{b}	2504 (318)^{a}	716 (106)^{b}	P (−)	0.006
N:P	39 (4)^{a}	13 (2)^{b}	40 (4)^{a}	10 (1)^{b}	P (−)	< 0.001
Roots (0–7.5 cm)						
%N	1.2 (0.11)	1.11 (0.08)	1.23 (0.13)	1.17 (0.04)	NS	
%C	43.96 (0.63)	44.88 (0.31)	43.41 (0.32)	43.12 (0.54)	Salinity (−)	0.024
%P	0.14 (0.02)	0.14 (0.01)	0.14 (0.02)	0.158 (0.01)	NS	
C:N	44.73 (4.39)	48.15 (3.21)	43.15 (4.05)	43.26 (1.6)	NS	
C:P	946.19 (139.35)	867.83 (73.82)	864.79 (87.75)	726.99 (87.75)	NS	
N:P	20.68 (1.44)	17.94 (0.51)	20.02 (0.51)	16.72 (1.09)	P (−)	0.033
Roots (7.5–15 cm)						
%N	1.19 (0.13)	1.03 (0.04)	1.00 (0.07)	1.13 (0.01)	NS	
%C	44.57 (0.22)^{a}	44.09 (0.56)^{ab}	43.21 (0.25)^{ab}	42.66 (0.50)^{b}	Salinity (−)	0.003
%P	0.130 (0.021)	0.133 (0.011)	0.113 (0.003)	0.133 (0.008)	NS	
C:N	46 (5)	51 (2)	52 (4)	46 (4)	NS	
C:P	1000 (142)	886 (87)	993 (30)	844 (46)	NS	
N:P	21 (1)	18 (2)	20 (1)	19 (2)	NS	

Average litter and root nutrient concentration and standard error (%C, %N, %P) and molar nutrient ratios (C:N, C:P, N:P). Treatment types: Fresh, Fresh + P, Salt, Salt + P. The driver and direction of effects and significant *P* values ($P < 0.05$) from two-way ANOVAs are included, and $P > 0.05$ is reported as NS (not significant). Superscripted letters represent results from Tukey's HSD test performed among our four individual treatments. If no letters are present, there were no significant differences between treatments

results may differ from chronic P additions over multiple years. Because sawgrass and periphyton have a finite ability to use P to produce biomass, a greater proportion of added P might be used by soil microbes for organic matter breakdown through time. In our study, added P was assimilated both by periphyton on the soil surface, without a shift in species composition (Mazzei et al., in review), and belowground sawgrass biomass increased without a change in stoichiometry, but greater P loading through time may lead to different outcomes. Furthermore, unlike nitrogen, P builds in soils once it exceeds the ability of the biota to sequester it where it can become remineralized and drive additional eutrophication through time (Qualls and Richardson 2008). Finally, through time, even low-level P loading can drive the dissolution of periphyton mats, modify consumer dynamics (Gaiser et al. 2005), and drive regime shifts in algal (Pan et al. 2000) and vegetation communities (Davis and Ogden 1994; Newman et al. 1996; Daoust and Childers 2004), with implications for OC dynamics and beyond.

Marsh Vulnerability and Everglades Restoration

Our research illustrates that increased freshwater delivery through restoration activities may enhance the capacity for freshwater and brackish coastal marshes to sequester and preserve OC and may improve the ability of wetlands to maintain elevation in the face of SLR. Accelerated rates of SLR are driving saltwater intrusion in coastal wetlands globally (Herbert et al. 2015), and some areas of South Florida have recorded SLR rates 2–6 times higher than the global average (Wdowinski et al. 2016; Dessu et al. 2018). Due to the combination of SLR and reduced freshwater flow (McVoy et al. 2011; Sklar et al. 2005), coastal wetlands in the Florida Everglades will continue to experience saltwater intrusion, and rapid peat collapse may be inevitable without intervention of freshwater delivery through restoration. Sawgrass marshes in the Everglades have increased their elevation at lower rates than current rates of SLR (Meeder et al. 2017), indicating that even without elevation loss from saltwater intrusion, marshes are at risk. However, increasing freshwater delivery, through Everglades restoration, can reduce salinity and restore inundation regimes where they have been altered and can slow or avoid rapid peat collapse in the near term, increasing the adaptive capacity of the ecosystem. The Comprehensive Everglades Restoration Plan seeks to counteract saltwater intrusion by increasing freshwater delivery to the coastal Everglades (Sklar et al. 2005), and our results suggest that freshwater restoration should be a high priority.

Although our study documents short-term (1 year) changes in coastal marshes with highly organic soils, our findings are likely relevant to many freshwater and brackish wetlands experiencing saltwater intrusion. For example, Weston et al. (2014) identified reduced soil C sequestration and total accretion rates in mineral soils in oligohaline and tidal freshwater marshes compared to long-term rates due to saltwater intrusion, even though average soil OC content was much lower than our peat-rich soils from this study (4.3–6.3% OC). Timing of vegetation shifts is essential because once elevation is lost, water depth may prevent vegetation establishment, as has been shown after plant die-offs in *Spartina alterniflora* marsh (Delaune et al. 1994; Schrift et al. 2008). Living roots play a critical role in soil elevation by increasing soil volume and stabilizing sediments, therefore preventing elevation loss; living roots must either be preserved or new plants must be recruited to replace soil volume (Baustian et al. 2012). Therefore, freshwater restoration can buy time for halophyte recruitment and transgression, increasing the likelihood that vegetated wetlands will persist. In particular, mangrove ecosystems are often capable of faster soil elevation gains than brackish sawgrass marshes (Meeder et al. 2017), but they require time to develop OC stocks (Osland et al. 2012). Finally, while there is concern that increasing freshwater restoration may submerge some coastal wetlands (Flower et al. 2017b), our results show that increasing inundation depth reduced root breakdown in brackish marshes with no change in root biomass or productivity, indicating that moderate inundation can promote OC accumulation.

Our results show that saltwater intrusion can cause loss of OC storage in highly organic coastal wetlands, driving a loss in soil elevation and perhaps conversion to open water. Wetlands store 20–30% of all soil C despite occupying only 5–8% of land area (Mitsch and Gosselink 2007; Nahlik and Fennessy 2016), but human activity has decreased wetland area by 50–87% in the last 300 years (Dahl 2011; Davidson et al. 2016). Many coastal wetlands have stored OC to maintain their elevation for millennia (Woodroffe 1990; McKee et al. 2007), but the acceleration of SLR will endanger the majority within this century (Kirwan and Megonigal 2013; Morris et al. 2016). Coastal wetland survival will depend on biophysical feedbacks between plants, soil, and the environment that increase soil elevation (Kirwan et al. 2016). Our results illustrate that saltwater intrusion is likely to reduce resilience to SLR by driving elevation loss, indicating that minimizing saltwater intrusion through the sustainable management of freshwater resources will be critical to freshwater and brackish coastal wetland survival in the coming century.

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