Can Saltwater Intrusion Accelerate Nutrient Export from Freshwater Wetland Soils? An Experimental Approach

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Coastal wetlands are vulnerable to saltwater intrusion, which may alter soil biogeochemical processes, lead to the export of nutrients into the coastal zone, and contribute to eutrophication. Using intact soil cores from three different freshwater wetlands and subjecting them to control (0), 5, or 15 parts per thousand (ppt) seawater treatments, we investigated how different wetland soils (bayhead swamp, cypress dome, and mineral marsh) and salinities alter the export of soil nutrients [soluble reactive P (SRP), NH_4^+, and dissolved organic C (DOC)], as well as microbial biomass C and greenhouse gas emissions. The highest salinity treatment increased CO_2 production by 30% with no change in methane production. Porewater NH_4^+ concentrations averaged 8× higher than the control in the 15-ppt treatment and 5× greater than the control in the 5-ppt treatment, with a ~1-wk lag period between porewater accumulation of NH_4^+ and export into the surrounding water. The magnitude of NH_4^+ export was mediated by wetland soil type. Soluble reactive P concentrations averaged 8× and 3.5× higher in the cypress dome and bayhead swamp 15-ppt treatments respectively than in their controls, though no effect was observed within the mineral marsh. Dissolved organic C concentrations differed by wetland soil type but were unaffected by salinity treatment. This study demonstrates that saltwater intrusion could catalyze the rapid export of nutrients from freshwater wetland soils into the coastal zone, though nutrient export varies by wetland soil type.

Abbreviations: CEC, cation exchange complex; DOC, dissolved organic C; MBC, microbial biomass C; ppt, parts per thousand; SRP, soluble reactive P.

The global sea level is rising at a rate of 3.2 ± 0.4 mm yr^{-1} and is estimated to result in a roughly 1-m increase by 2100 (Church et al., 2013; Intergovernmental Panel on Climate Change, 2014), which has implications for the salinization of coastal and inland landscapes. Specifically, the low-lying coastal plain is particularly vulnerable to this amplified rate of sea level rise, including tidal freshwater coastal wetlands that occupy the terrestrial interface between the coastal ocean and upland areas and were developed under conditions of low salinity and minimal tidal inundation. As one of the most productive ecosystem types on the planet, coastal wetlands provide a critical habitat for wetland biota, regulate water quality, sequester C, and act as a buffer during storm events (Barbier et al., 2011). Sea level rise is estimated to result in the loss of 20 to 30% of the global extent of coastal wetlands and their critical services by 2100 (Nicholls et al., 1999). In response to sea level rise, coastal wetlands may transgress landward: brackish marshes may become more saline and inundated and saltwater may intrude into tidal freshwater wetlands (Neubauer and Craft, 2009). Saltwater intrusion can have effects on all components of the wetland, including shifts vegetation communities, loss of habitat, changes in the microbial consortia, and disruption of biogeochemical cycles (Herbert et al., 2015).

Core Ideas

- Ammonium that accumulated in the porewater following an influx of seawater took ~1 wk to flux into the surrounding water.

- Soluble reactive P concentrations in both the porewater and surrounding water increased with salinity.

- Nutrient export was influenced by wetland soil type.

- Saltwater intrusion could catalyze the rapid export of nutrients from freshwater wetland soils into the coastal zone, especially in organic matter-rich soils.

Sea level rise has sparked a variety of research addressing the effects of saltwater intrusion on the cycling of C, N, and P in coastal wetlands. Many of these studies have been controlled laboratory experiments that subjected soils from either tidally-influenced freshwater or brackish wetlands to increases in inundation, seawater, or both (Chambers et al., 2011, 2013, 2014; Weston et al., 2006, 2011; Jun et al., 2013; Marton et al., 2012; van Dijk et al., 2015). It is important to note the difference between increases in salinity (i.e., salts, such as NaCl) and saltwater intrusion, which contains sulfate, a terminal electron acceptor. For ease of understanding, "salinity" will henceforth refer to the influx of seawater containing sulfate. Previous short-term experiments suggest that subjecting soils to seawater can affect both abiotic and biotic drivers of biogeochemical cycling within freshwater wetlands. Abiotic effects result from the influx of high concentrations of ions brought into the system by saline water: Na^+, Cl^-, SO_4^{2-}, Mg^{2+}, Ca^{2+}, and K^+. On a timescale of hours to days, these ions have the potential to disrupt the chemical equilibrium of the system, alter the solubility of minerals and gases, and promote flocculation of particles (Stumm and Morgan, 1996; Sholkovitz, 1976; Gardner et al., 1991). Biotic effects often result from abiotic changes and can include microbial responses such as increased respiration arising from the influx of bioavailable nutrients or terminal electron acceptors, as well as vegetation responses such as landward transgression of saline-tolerant communities (Chambers et al., 2013). Microbiota are also affected by the osmotic stress associated with increased ionic concentrations, and respond with decreased respiration rates and decreased microbial diversity (Baldwin et al., 2006).

Despite the amount of literature available on the effects of saltwater intrusion on wetland soils, there are still conflicting reports regarding respiration and C mineralization, largely because of differences in experimental design (e.g., salinity regimes) and the time-scale of the experiments (Chambers et al., 2011, 2013, 2014; Weston et al., 2006, 2011). The majority of these studies have shown increases in CO_2 production with the influx of seawater into either tidally influenced freshwater wetlands or brackish wetlands (Chambers et al., 2011, 2014; Weston et al., 2006, 2011; Marton et al., 2012). Saltwater intrusion into freshwater wetlands increases the availability of sulfate, an abundant ion in seawater that serves as a terminal electron acceptor during anaerobic microbial respiration. The influx of sulfate influences the redox potential of soils to thermodynamically favor sulfate reduction over other respiration pathways and therefore increases CO_2 production (Reddy and DeLaune, 2008). Tidal freshwater wetlands are known to be sources of CH_4, a greenhouse gas with 25 times the radiative forcing potential of CO_2 because of the high electron pressure and available organic matter (Intergovernmental Panel on Climate Change, 2014). Most studies report that with an influx of seawater, brackish or tidal freshwater wetlands produce less CH_4 because of shifting respiration pathways, though the magnitude of the salinity change and the time-scale of the experiment can alter the effect (Chambers et al., 2011, 2014; Weston et al., 2006; Poffenbarger et al., 2011; Neubauer et al., 2013; Marton et al., 2012). However, in one tidal laboratory study with increased

salinity (5 ppt), Weston et al. (2011) observed an increase in CH_4 emissions from tidal freshwater marsh soil cores over a 1-yr period.

Dissolved organic C is another C loss pathway that may be affected by increased salinity. Studies indicate that DOC concentrations may be unaffected by changes in salinity (Weston et al., 2006, 2014) or decreased with elevated salinity (Chambers et al., 2013; Ardón et al., 2016). Salts can stimulate flocculation of DOC, resulting in the transformation of DOC into particulate organic C (Ardón et al., 2016). Clearly, the effects of increasing salinity on C loss (CO_2, CH_4, and DOC) in wetland soils have yet to be fully understood and most probably depend on other factors, such as soil type, salinity concentration, substrate quality, dominant vegetation, hydrologic fluctuations, and nutrient availability.

Increases in salinity can also have implications for changes in P cycling. Phosphorus cycling is regulated by adsorption–desorption, flocculation–dissolution, and ionic exchange (Reddy et al., 1999). Phosphorus availability is highly influenced by the pH of the system; increases in salt concentrations or influx of seawater can decrease pH (Weston et al., 2006; Chambers et al., 2011). Moreover, increases in sulfate concentrations in the water column can lead to the dissolution of minerals containing Fe and the subsequent release of P bound to Fe. In a laboratory study coupled with a field component, Jun et al. (2013) documented decreases in P concentrations via promotion of sorption after a 2- to 3-ppt salinity increase in a tidal freshwater floodplain forest after ~1 wk. Similar results were reported by Weston et al. (2006), during which freshwater wetland sediments were subjected to a 10-ppt increase in salinity that resulted in an initial decrease in HPO_4^{2-} porewater concentrations, followed by a subsequent increase after 15 d, indicating that the duration of saltwater intrusion has ramifications for P availability. In contrast, exposure of a tidal freshwater marsh to a 5-ppt increase in salinity over 1 yr resulted in no significant change to phosphate concentrations (Weston et al., 2011). However, a laboratory study investigating salinity pulses on freshwater, brackish, and salt marshes documented greater SRP release within the freshwater and brackish marshes (Chambers et al., 2013).

The most well documented effect of increasing salinity on wetland soils may be the nearly immediate liberation of ammonium (NH_4^+) from the soil and into the porewater. Ammonium is the most prevalent species of N in anaerobic environments and adheres to the soil cation exchange complex (CEC). Ammonium is stripped from the CEC within hours and replaced with divalent or monovalent ions present in seawater with the influx of ions from increased salinity. (Rysgaard et al., 1999; Seitzinger et al., 1991; Weston et al., 2006; Ardón et al., 2013; Jun et al., 2013). What remains unknown is how salinity and wetland soil type impact how much of this NH_4^+ is subsequently nitrified or assimilated within the soil, versus how much diffuses into the surrounding surface water and is exported from the system.

This study seeks to quantify the effects of seawater intrusion on the export of bioavailable nutrients (DOC, SRP, and NH_4^+) and the production of greenhouse gases in three different types of freshwater wetland soils with varying physiochemical properties, specifically organic matter content. If nutrients released into

the porewater through the biotic and abiotic processes described above are released into the surrounding water column and, subsequently, the coastal zone (facilitated by tidal flow), there could be far-reaching ecosystem-level implications. Increases in N and P can reduce limitations on phytoplankton growth in the coastal ocean and contribute to harmful algal blooms and associated hypoxia (Turner and Allen, 1982).

METHODS
Experimental Design

To understand the effects of salinity on nutrient dynamics, we selected sites in three different types of freshwater wetlands in east-central Florida: a cypress dome (28°36′30.4″N, 81°11′57.16″W), a bayhead swamp (28°36′22.95″N, 81°12′6.77″W), and a mineral marsh (28°35′30.40″N, 81°10′46.88″W). Site selection was based on the desire to obtain a varying range in soil organic matter. Soils at the cypress dome site were classified as Sanibel muck (sandy, siliceous, hyperthermic Histic Humaquepts) and had a 10-cm overlying water column. The dominant vegetation was *Taxodium distichum* (L.) Rich. Soils at the bayhead swamp site were within the same taxonomic classification and although there was no overlying water column, the soils were saturated. The dominant vegetation species were *Persea palustris* (Raf.) Sarg. and *Myrica cerifera* L. The dominant vegetation at the mineral marsh site was *Eleocharis* spp. and a 10-cm water column overlayed Basinger fine sand soils (siliceous, hyperthermic Spodic Psammaquents). Intact cores were collected in polyvinyl chloride tubes 25 cm long and 10 cm wide, each with nine holes 127 mm in diameter, predrilled at randomly spaced intervals around the tube. Cores were collected to a depth of 15 cm via the push coring method. Immediately after removal from the natural environment, cores were wrapped in cling wrap to prevent water drainage through the holes and to preserve anaerobic conditions, then plugged at the bottom with a mechanical stopper. Twelve field-replicate cores from each site

were placed on ice and transported back to the laboratory. Once the intact soil cores arrived at the lab, they were sorted by site and flooded with a 5-cm water column for a 24-h acclimation period before the start of the experiment.

Prior to beginning the experiment, water was obtained from Lake Claire (28°36′27.53″N, 81°12′9.71″W), a shallow lake located in close proximity to the three wetland sites and fed by the same surface and groundwater as the sampling sites. Water from the lake was pumped through a series of 10-, 5-, and 1-μm filters to remove particulates and was stored in five 20-L Nalgene carboys (Nalgene, Rochester, NY) prior to addition of the soil cores. The two salinity treatments (5 and 15 ppt) were created by adding TropicMarin sea salt (Tropic Marin, Wartenburg, Germany) to the water stored in the carboys to obtain the appropriate salinity, and then the solution was mixed for 10 min.

All cores were placed in individual water baths comprising a larger polyvinyl chloride tube (15.24 cm in diameter) with a watertight cap at the bottom. A 6.35-mm pumice air stone was then inserted into each core at a depth of 10 cm and attached to a silicon tube 15 cm long connected to a 20-mL syringe to obtain porewater samples (Fig. 1). The individual water baths were filled with water of an appropriate salinity treatment and a 5-cm water column was maintained above the soil surface. Each salinity treatment included four replicates from each site (bayhead swamp, cypress dome, and mineral marsh). Over a 3-wk period, the water bath was drained and replaced weekly with filtered water from the nearby lake at the appropriate salinity for the treatment.

Nutrient Sampling

Porewater samples were collected via the airstone connected to a 20-mL syringe seven times over the course of the 3-wk experiment, and eight times from the surrounding water bath (Table 1). Twenty mL of water was extracted, immediately filtered through a Supor 0.45-μM filter (Pall Corporation, Port Washington, NY) and acidified with distilled, deionized H_2SO_4 to a pH of <2. Temperature, pH, and conductivity measurements were obtained immediately prior to each sampling event over the course of the experiment with an Accumet bench top pH probe (Accumet XL200, ThermoFisher Scientific, Waltham,
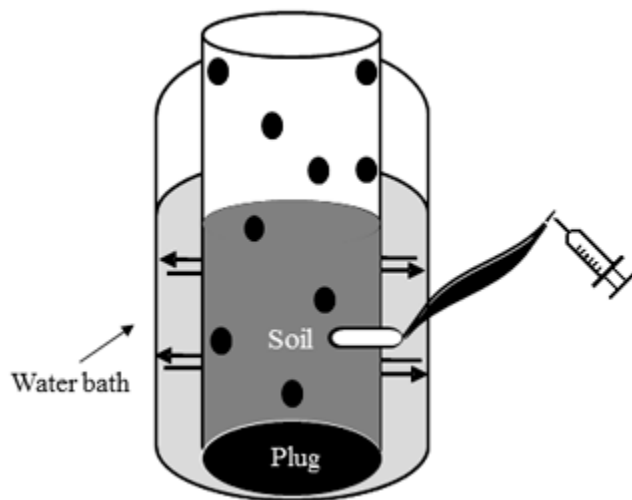

Fig. 1. Diagram of core setup. Each soil core had nine 127-mm holes drilled at random into the core tube and was contained within a capped 15.24-cm polyvinyl chloride water bath. A 6.35-mm-long air stone was inserted into the cores at a depth of 10 cm and attached to a 15-cm silicon tube connected to a 20-mL syringe.

Table 1. Timeline for each sampling and water change that took place over the course of the experiment.

Day	Sampling
1	Porewater and leachate
2	Porewater and leachate
4	Porewater, change water†
5	Leachate
7	Porewater and leachate
11	Porewater, change water
12	Leachate
14	Porewater and leachate
18	Porewater, change water
19	Leachate
21	Porewater and leachate

† The changed water was sampled to provide a baseline for nutrient levels throughout the experiment.

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MA). After each sampling, filtered lake water of the appropriate salinity was added to the water bath to maintain a constant water column height of 5 cm above the soil surface.

The surrounding water column, porewater, and filtered Lake Claire water samples were analyzed for DOC on a Shimadzu TOC-L Analyzer (Kyoto, Japan). Samples were analyzed for ammonium N (NH_4^+–N) and SRP on a SEAL AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI) via EPA Methods 350.1 Rev. 2 and 365.1 Rev. 2, respectively (USEPA, 1993). Samples were also analyzed for NO_x (nitrate + nitrite) on the Seal AQ2 via USEPA Method 353.1 Rev. 2.0 (USEPA, 1993) but the concentrations were consistently below the detection limit (0.003 mg NO_x L^{-1}) and are therefore not discussed.

Soil Physiochemical Properties

At the end of the laboratory experiment, soils were destructively sampled and extruded to three depths (0–5 cm, 5–10 cm, and 10+ cm). Each sample was immediately weighed and stored at 4°C to be analyzed for physiochemical properties. Gravimetric moisture content was determined by homogenizing the field-moist soil samples and placing them in a forced air oven at 70°C for 3 d until a constant weight was achieved. Bulk density was calculated from the percentage of moisture and expressed on a dry weight basis. Dried soils were ground with a SPEX Sample Prep 8000M Mixer/Mill (SPEX Certiprep, Metuchen, NJ). Dried and ground subsamples were used to determine total C and N on a Vario Micro Cube CHNS Analyzer (Elementar Americas Inc., Mount Laurel, NJ). Solid-phase total soil P analysis was performed by combusting dried subsamples at 550°C for 5 h to determine the percentage organic matter via loss-on-ignition, boiling the resulting ash in 1 N HCl on a hot plate for 30 min, and subsequent filtration through Whatman #41 filters (Andersen, 1976). Samples were then analyzed on an AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI) via USEPA Method 365.1 Rev. 2 (USEPA, 1993). Extractable NH_4^+ concentrations were determined by placing 2.5 g of field-moist soil into a 40-mL centrifuge tube, adding 25 mL of 2 M KCl and agitating the sample on an orbital shaker at 100 rpm for 1 h. Samples were then centrifuged for 10 min at 4000 rpm and 10°C. The supernatant was filtered through Supor 0.45-μM filters (Pall Corporation), acidified with distilled, deionized H_2SO_4 to a pH of <2, and analyzed for NH_4^+–N within 30 d (Roy and White, 2013).

Microbial Biomass C

Microbial biomass C (MBC) was determined via the chloroform fumigation method after Vance et al. (1987). Microbial biomass C analysis was performed on the 0- to 5-cm depth segment for each sample by weighing 2.5 g of field-moist soil into 40-mL centrifuge tubes in duplicate. One set of samples was fumigated with chloroform for 24 h in a glass vacuum desiccator. The nonfumigated control set was extracted with 25 mL of 0.5M K_2SO_4, agitated continuously for 1 h at 100 rpm on an orbital shaker, and centrifuged for 10 min at 10°C and 4000 rpm. The supernatant was decanted and vacuum-filtered through Supor

0.45 μM filters (Pall Corporation). The samples were then acidified with distilled, deionized H_2SO_4 to a pH of <2 and analyzed within 30 d. Following 24 h of chloroform fumigation, the fumigate samples were analyzed in the same method as the nonfumigated samples. A Shimadzu TOC-L Analyzer (Shimadzu Instruments, Kyoto, Japan) was used to determine nonpurgeable organic C for each set of samples. Microbial biomass C was calculated as the difference in nonpurgeable organic C between the fumigated samples and the nonfumigated samples.

Respiration: CO_2 and Methane

Respiration rates were obtained by weighing 7 g of field-moist soil (0–5 cm) into glass serum bottles and capping them with rubber septa and aluminum crimps. Bottles were evacuated to 75 cmHg and purged for 3 min with 99.99% O_2–free N_2 gas. Fifteen mL of N_2–purged site water was injected into each sample. Bottles were shaken continuously on an orbital shaker at 100 rpm and 25°C for 1 h. Gas samples were extracted using gas-tight syringes every hour for a 4-h period and injected into a GC-2014 Gas Chromatograph (Shimadzu Instruments).

Statistical Analysis

Data analysis was performed via a three-way ANOVA in R (R Foundation for Statistical Computing, Vienna, Austria) to determine the effects of wetland soil type, salinity, depth, and their interactions. The Shapiro–Wilks test was used to determine whether the soil physiochemical data met the assumptions of normality and Levene's test was used to determine the homogeneity of variance. Greenhouse gas efflux (CH_4 respiration and CO_2 respiration) and MBC data were analyzed with an ANOVA in R to determine the effects of wetland soil type, salinity, and the interaction between the two. These data were transformed with a square-root transformation to meet the assumption of normality (the Shapiro–Wilk test). Nutrient data (both nutrient concentrations in the porewater and in the surrounding water) and environmental conditions (temperature, pH, and conductivity) were analyzed in R via a repeated-measures ANOVA to determine the effects of wetland soil type, salinity, and the interaction between the two. The variable 'week' was added to account for the each time the water in the mesocosms was replenished and treated as a covariate. The total concentration of each nutrient within the porewater was determined by summing the average concentration of each nutrient in the porewater at each sampling time. The total concentration of each nutrient within the surrounding water was calculated in the same manner. To determine the percentage of each nutrient that that was exported into the surrounding water from the porewater, the total in the surrounding water was then divided by the total in the porewater and the resulting decimal was multiplied by 100 to yield a percentage.

RESULTS
Soil Physiochemical Properties

The percentage moisture content and bulk density varied with the three-way interaction between wetland soil type, salinity,

Table 2. Control soil physiochemical properties by wetland soil type and depth. All physiochemical properties differ significantly among wetland soil types.

Wetland soil type	Depth	Moisture content		Bulk density		Organic matter		Total C		Total N		Total P		Extractable NH$_4^+$	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
	cm			—g cm^{-3}—		—%—		—g kg^{-1}—		—g kg^{-1}—		—mg kg^{-1}—		—mg L^{-1}—	
Bayhead swamp	0–5	0.85	0.01	0.11	0.01	92.54	2.82	455.83	4.34	13.03	1.53	618.11	131.52	126.67	33.32
	5–10	0.87	0.00	0.11	0.01	85.72	2.24	443.35	11.85	12.15	0.64	510.76	17.94	117.08	23.40
	10+	0.85	0.00	0.14	0.01	75.90	4.23	417.05	11.99	13.05	0.92	525.06	54.18	107.97	40.22
Cypress dome	0–5	0.75	0.02	0.23	0.03	47.91	4.39	250.88	25.13	9.83	1.11	352.17	35.79	60.43	4.40
	5–10	0.66	0.03	0.37	0.05	31.13	3.98	161.53	13.56	7.93	0.23	449.72	126.83	31.54	4.62
	10+	0.55	0.04	0.57	0.06	19.86	4.44	111.97	1.83	5.51	0.29	191.37	17.61	21.88	5.79
Mineral marsh	0–5	0.37	0.02	0.75	0.03	8.31	1.42	64.78	8.29	3.58	0.60	51.63	11.22	16.81	2.05
	5–10	0.22	0.01	1.34	0.09	2.54	0.93	10.53	5.72	0.65	0.27	56.63	27.37	0.40	0.21
	10+	0.12	0.06	1.83	0.06	0.91	0.23	1.83	0.48	0.27	0.03	76.17	1.67	8.61	7.76

and depth ($p < 0.01$ and $p < 0.001$, respectively). Generally, the highest moisture content occurred in the bayhead swamp and the lowest moisture content was found in the mineral marsh; moisture content decreased with depth (Table 2). Moisture content was negatively correlated with bulk density and positively correlated with total C, N, and P, and the percentage of organic matter (Table 3). Bulk density ranged from 1.83 ± 0.06 g cm^{-3} in the control mineral marsh treatment at the 10$^+$-cm depth interval to 0.11 ± 0.01 g cm^{-3} in the control bayhead swamp treatments at the 5- to 10-cm depth interval. Bulk density was also negatively correlated with total C, N, and P, and the percentage of organic matter (Table 3). The interaction between wetland soil type and salinity influenced the pH of the water column, which varied from 7.89 ± 0.08 in the bayhead swamp 15-ppt treatment and 6.87 ± 0.05 the cypress dome 5-ppt treatment; increases in salinity contributed to increases in pH. Organic matter content varied among wetland soil types ($p < 0.001$), with the average organic matter contents of 4.03 ± 0.83, 37.89 ± 2.99, and $82.49 \pm 1.11\%$ in the mineral marsh, cypress dome, and bayhead swamp, respectively (Table 2). Organic matter content significantly decreased with depth. The percentage organic matter showed a strong positive correlation with total C, N, and P, and extractable NH$_4^+$ concentrations (Table 3).

Total C differed with wetland soil type ($p < 0.001$) and ranged from 405 ± 7.99 g kg^{-1} in the bayhead swamp to 35.0 ± 10.5 g kg^{-1} in the mineral marsh (Table 2). As depth increased, total C decreased ($p < 0.01$). Total N varied among wetland soil types ($p < 0.001$) and was highest in the bayhead swamp at 12.3 ± 0.34 g kg^{-1} and lowest in the mineral marsh at 2.71 ± 1.37 g kg^{-1} (Table 2). Total P also differed by wetland soil type ($p > 0.001$) in the same manner as total N: it was highest in the bayhead swamp

and lowest in the mineral marsh (Table 2). Strong positive correlations existed among total C, N, and P (Table 3).

The interaction between wetland soil type and salinity resulted in changes in soil-extractable NH$_4^+$ concentrations ($p < 0.001$). Concentrations ranged from a high of 117.2 ± 17.4 mg g^{-1} in the bayhead swamp control treatment to a low of 5.0 ± 1.6 mg g^{-1} in the mineral marsh 5-ppt treatment (Table 2). Extractable NH$_4^+$ concentrations also differed with depth ($p < 0.01$), being lower in the 10+ cm depth interval (47.2 ± 8.6 mg g^{-1}) than the 0- to 5-cm depth interval (67.5 ± 8.2 mg g^{-1}). Extractable NH$_4^+$ was negatively correlated with bulk density and positively correlated with moisture content, total C, N, and P (Table 3).

Microbial Biomass

Wetland soil type significantly affected MBC (0–5 cm; $p < 0.001$). Specifically, the cypress dome and bayhead swamp had higher MBC than the mineral marsh ($p < 0.001$; Fig. 2). The lowest average MBC occurred in the mineral marsh with 258 ± 92.0 mg g^{-1}, whereas the highest was found within the bayhead swamp with 1807 ± 297 mg g^{-1}. The MBC in the cypress dome was 1750 ± 216 mg g^{-1}, which was not significantly different from that in the bayhead swamp. The main effect of salinity was also significant ($p < 0.01$): the average MBC was higher (1678 ± 297 mg g^{-1}) in the 15-ppt treatment than in the 5-ppt treatment (1378 ± 336 mg g^{-1}) and in the control treatment (1034 ± 212 mg g^{-1}). Microbial biomass C was positively correlated with both the rate of CH$_4$ production and the rate of CO$_2$ production (Table 4).

Greenhouse Gas Production

The rate of CH$_4$ production (0–5 cm) did not differ significantly with salinity treatment but differed by wetland soil type ($p < 0.001$, Fig. 2). Average methane production in both the cypress dome (4.81 ± 1.45 μg CH$_4$–C g^{-1} h^{-1}) and the bayhead

Table 3. Correlation table of soil physiochemical measurements (degrees of freedom = 108; at $r = 0.197$, $p = 0.05$; at $r = 0.256$, $p = 0.01$). All values are significant.

	Extractable NH$_4^+$	Moisture content	Bulk density	Total C	Total N	Organic matter
Moisture content	0.723	–	–	–	–	–
Bulk density	–0.675	–0.960	–	–	–	–
Total C	0.681	0.797	–0.751	–	–	–
Total N	0.548	0.620	–0.588	0.744	–	–
Organic matter	0.755	0.844	–0.783	0.928	0.639	–
Total P	0.562	0.489	–0.473	0.538	0.628	0.592

Table 4. Correlation table of microbial biomass C and greenhouse gas analyses (degrees of freedom = 35; $\alpha = 0.05$; $r = 0.283$).

	Microbial biomass C	CH$_4$ respiration
CH$_4$ respiration	**0.316†**	–
CO$_2$ respiration	**0.512**	0.273

† Values in bold are significant.

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swamp (3.50 ± 0.19 µg CH_4–C g^{-1} h^{-1}) exceeded that of the mineral marsh (0.22 ± 0.12 µg CH_4–C g^{-1} h^{-1}; $p < 0.01$). The rate of CO_2 production (0–5 cm) varied with salinity treatment ($p = 0.05$) and wetland soil type ($p < 0.001$, Fig. 2). The highest rates were observed in the bayhead swamp (17.23 ± 2.37 µg CO_2–C g^{-1} h^{-1}) and the lowest rates were observed within the mineral marsh (0.95 ± 0.51 µg CO_2–C g^{-1} h^{-1}). Between the 0-ppt and 15-ppt treatments, CO_2 rates changed significantly ($p < 0.05$), ranging from an average of 11.46 ± 3.59 µg CO_2–C g^{-1} h^{-1} in the 15-ppt treatment to 6.86 ± 2.02 µg CO_2–C g^{-1} h^{-1} in the 0-ppt treatment.

Nutrient Export
Porewater Nutrients

Porewater NH_4^+ concentrations differed with the interaction between wetland soil type and salinity treatment ($p < 0.001$, Fig. 3a). In all three wetland soil types, the 15-ppt salinity treatment contained the highest average porewater NH_4^+ concentration (2.43 ± 0.33 to 2.99 ± 0.40 mg L^{-1}), followed by the 5-ppt treatment (1.16 ± 0.17 to 2.27 ± 0.26 mg L^{-1}), both of which were always significantly greater than the control (0.25 ± 0.02 to 0.44 ± 0.07 mg L^{-1}). Specifically, the average porewater NH_4^+ concentrations in the 15-ppt treatment ranged from 5× (bayhead swamp) to 12× (cypress dome) than that in the control, whereas the 5-ppt treatment ranged from 2× (bayhead swamp) to 9× (cypress dome) than that in the control. Generally, NH_4^+ concentrations in the porewater increased with increasing salinity almost immediately (i.e., within 1 d after salinity addition), reaching a peak in Week 3.

Concentrations of SRP in the porewater differed with the interaction between wetland soil type and salinity ($p < 0.001$), ranging from a high of 0.42 ± 0.11 mg L^{-1} in the 15-ppt mineral marsh to a low of 0.018 ± 0.001 mg L^{-1} in the 15-ppt bayhead swamp (Fig. 3b). Both the cypress dome and the mineral marsh showed a similar pattern of increasing SRP with increasing salinity, with the highest concentrations seen in the mineral marsh. In contrast, the bayhead swamp had the lowest porewater SRP in the 15-ppt treatment, but the effect of salinity was not significantly different from the control. Porewater SRP was not significantly correlated with week.

Dissolved organic C concentrations in the porewater changed with the interaction between wetland soil type and salinity ($p < 0.001$), ranging from 29.16 ± 2.08 mg L^{-1} in the cypress dome 15-ppt treatment to 15.39 ± 0.706 mg L^{-1} in the bayhead swamp 15-ppt treatment (Fig. 3c). In the bayhead swamp, DOC concentrations were highest in the control treatment and decreased slightly with increasing salinity. However, in both the cypress dome and mineral marsh wetland soil types, the 15-ppt treatment had the greatest average DOC concentrations. Overall, the concentration of DOC in the porewater was greatest in the control treatments in Week 1 and gradually decreased until Week 3.

Water Column Nutrients

Salinity had a significant effect on water column NH_4^+ concentrations within the surrounding water bath ($p < 0.001$, Fig. 4a). Concentrations of NH_4^+ in the 15-ppt treatment ranged from
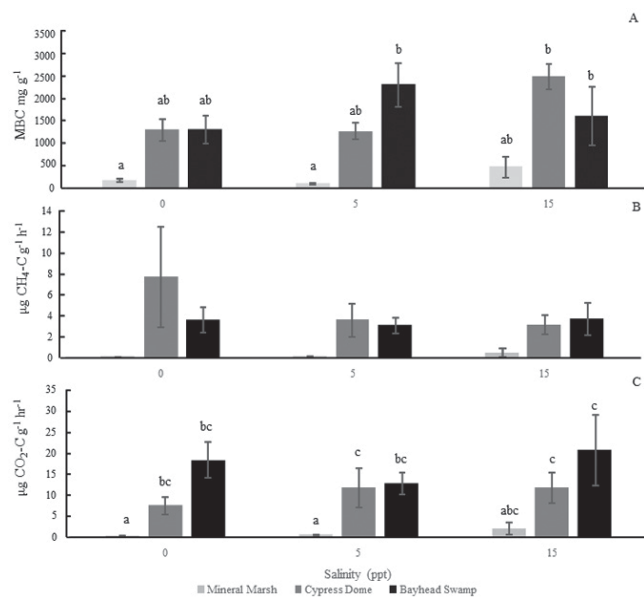

Fig. 2. Microbial biomass C (a), CH_4 production (b), and CO_2 production (c) with regards to salinity and wetland soil type. Data are shown as means ± 1 SE ($n = 4$). Letters denote significant differences among wetland soil types and salinity treatments.
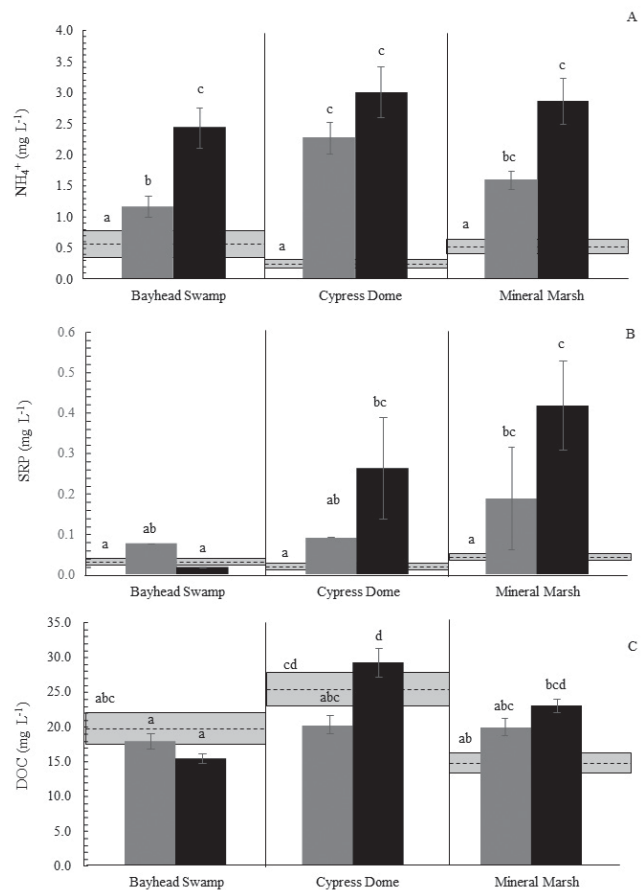

Fig. 3. Average NH_4^+ (A), soluble reactive P (SRP) (B), and dissolved organic C (DOC) (C) concentrations in the porewater by both salinity and wetland soil type. Letters denote significance. Control treatments ± 1 SE are denoted by horizontal bars. Gray vertical bars indicate the mean and SE of the 5-parts per thousand (ppt) treatment and black vertical bars indicate the mean and SE of the 15-ppt treatment.

4× (bayhead swamp) to 8.7× (cypress dome) higher than that in the controls, whereas the 5-ppt treatment ranged from 2.7× (bayhead swamp) to 5.3× (cypress dome) than that in the controls. Time also affected NH_4^+ export into the water column, with the highest concentrations observed between Weeks 1 and 2 of the 3-wk study in both the 15- and 5-ppt treatments. Over the course of the experiment, the highest percentage of total NH_4^+ that was exported from the porewater into the surrounding water column was seen in the 5-ppt bayhead swamp treatment (95%), whereas the lowest export was observed in the 5-ppt mineral marsh treatment (32%, Table 5). With the exception of the bayhead swamp, the percentage of porewater that was exported into the surrounding water was highest in the 15-ppt salinity treatment.

Soluble reactive P in the water column varied with the interaction between salinity and wetland soil type ($p < 0.01$, Fig. 4b). The greatest average water column SRP concentrations were observed in the 15-ppt cypress dome treatment (0.20 ± 0.12 mg L^{-1}) and the lowest were seen in the 5-ppt cypress dome treatment (0.01 ± 0.002 mg L^{-1}). The concentration of SRP averaged 8× higher and 3.5× higher respectively in the cypress dome and bayhead swamp 15-ppt treatments than in their respective controls. In the mineral marsh, neither of the salinity treatments differed significantly from the control. Export of SRP

out of the porewater and into the surrounding water was highest in the bayhead swamp 15-ppt treatment (103%) and lowest in the 15-ppt cypress dome treatment (2%, Table 5). Week was not a significant influence on SRP concentrations.

Concentrations of DOC in the water column around the soil cores varied among the wetland soil types ($p < 0.01$, Fig. 4c), with the highest average concentrations observed in the cypress dome (21.71 ± 2.41 mg L^{-1}) and the lowest average concentrations found in the bayhead swamp (15.87 ± 1.54 mg L^{-1}). Time (week) was also a significant influence on water column DOC concentrations, though the effect was considered an artifact of the experimental design and treated as a covariate (see discussion). Dissolved organic C in the water column was highest during the first week and then decreased during Week 2. After Week 2, the DOC concentrations were stable for the remainder of the experiment. Total export of DOC out of the porewater and into the surrounding water was highest in the 15-ppt bayhead swamp treatment (82%) and lowest within the 15-ppt mineral marsh (24%, Table 5).

DISCUSSION

We used soils from three different freshwater wetland soil types and monitored the export of nutrients from the porewater into the surrounding water column over time in an effort to more fully understand how both wetland soil type and increases in salinity (as a product of sea level rise) affect the potential export of labile soil nutrients through both horizontal flow (mimicking tidal fluctuations) and diffusion. A variety of controlled laboratory studies have been conducted to determine the short-term effects of increased salinity on freshwater wetland soils, though these studies have focused primarily on the response of the porewater nutrients to salinity changes, or how greenhouse gas production changes over time (e.g., Ardón et al., 2013, 2016; Baldwin et al., 2006; Bartlett et al., 1987; Chambers et al., 2011, 2013, 2014; Jun et al., 2013; Marton et al., 2012, Poffenbarger et al., 2011; van Dijk et al., 2015; Weston et al., 2006, 2011). Generally, these studies have been conducted on one wetland soil type and few studies have examined how wetland soil type and organic matter content (and properties correlated to organic matter) impact the response to increases in salinity. We found that wetland soil type significantly affected how soils respond to increasing salinity, specifically in regards to export of nutrients and greenhouse gas production.

In terms of soil physiochemical parameters, the mineral marsh represented the lowest amount of elemental C, N, and P
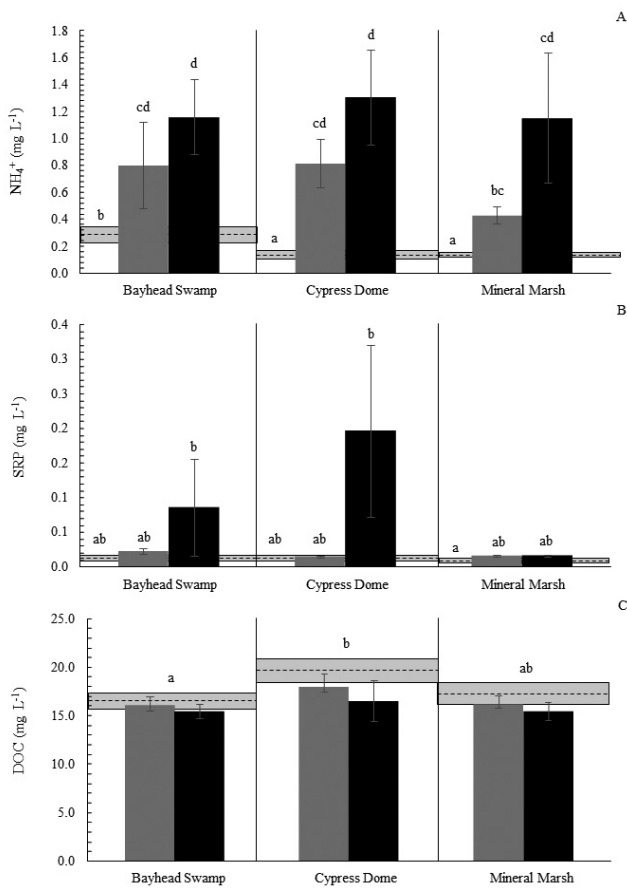

Fig. 4. Average NH_4^+ (A), soluble reactive P (SRP) (B), and dissolved organic C (DOC) (C) concentrations in the surrounding water by both salinity and wetland soil type. Letters denote significance. Control treatments ± 1 SE are denoted by horizontal bars. Gray vertical bars indicate the mean and SE of the 5-parts per thousand (ppt) treatment and black vertical bars indicate the mean and SE of the 15-ppt treatment.

Table 5. Percentage of total porewater nutrients [NH_4^+, soluble reactive P (SRP), dissolved organic C (DOC)] that was exported from the porewater to the surrounding water over the course of the experiment.

Wetland soil type	Salinity	NH$_4$	SRP	DOC
	parts per thousand		%	
Bayhead swamp	5	94.7	82.9	82.1
	15	66.0	103.0	96.7
Cypress dome	5	57.3	55.9	75.0
	15	84.0	2.0	26.7
Mineral marsh	5	32.3	12.0	55.0
	15	81.0	6.6	24.3

within the soil, as well as low organic matter content, low moisture content, and high bulk density compared with the other wetland soil types. Consequently, the rates of CH_4 and CO_2 production were lowest at this site because of the lack of soil organic matter available to provide an electron donor to support high respiration rates (Reddy and DeLaune, 2008). Likewise, MBC was also significantly lower in the mineral marsh than in either of the other treatments. In general, the mineral marsh was observed to have a larger particle size than the other two wetland soil types (grain size = 2.94 in diameter; Steinmuller, unpublished data, 2016). The large particle size of sand promotes shorter path lengths for oxygen diffusion and higher hydraulic conductivity, and sandy soils are thus more aerated than organic-rich soils (Brady and Weil, 2010). Sandy soils also lack the electrochemical charges associated with clay and organic soils that adhere nutrients to the soil.

Carbon Dynamics

Average CO_2 respiration rates generally increased with increasing salinity across all wetland soil types. The influx of sulfate associated with elevated salinity influences the redox potential of wetland soils to use sulfate as an alternate electron acceptor for respiration, a pathway that is thermodynamically favored over methanogenesis and results in an increase in CO_2 production (Reddy and DeLaune, 2008). This finding is consistent with several previous studies, all of which have found accelerated CO_2 respiration rates after exposing freshwater soils to increases in seawater (Chambers et al., 2011; Weston et al., 2006, 2011; Marton et al., 2012). Microbial biomass C was greater in the 15-ppt treatment than the other two treatments and was significantly correlated with CO_2 production. Other studies have also found higher microbial biomass in more saline coastal wetland soils (Chambers et al., 2013), which may be attributed to the increasing abundance of sulfate reducers, despite the limitations imposed by the osmotic stress associated with the influx of ions within seawater (i.e., Baldwin et al., 2006).

Previous studies have also suggested that implementation of brackish and saline salinity regimes (>10 to 18 ppt) catalyzes a decrease in CH_4 production because of the competitive inhibition by sulfate reducers (e.g., Weston et al. 2006; Chambers et al., 2011; Neubauer et al., 2013). However, CH_4 production was not significantly affected by changes in salinity (up to 15 ppt) in this study. Others have found that methanogenesis can occur concomitantly with sulfate reduction as long as the methanogenic bacteria use noncompetitive substrates (i.e., substrates that are not suitable electron donors for sulfate reduction), which may explain our findings (Capone and Kiene, 1988). Average CH_4 production rates in the control treatments were roughly 50% lower than the CO_2 respiration rates, indicating that methanogenesis is not the dominant pathway for respiration under ambient salinity. Roden and Wetzel (1996) concluded that sulfate reduction and methanogenesis were responsible for 4 and 29% of mineralized C in freshwater wetlands respectively, whereas reduction of Fe accounted for roughly 67%. In contrast, sulfate reduction can constitute up to 95% of the organic C oxidation in freshwater sedi-

ments exposed to 10 ppt seawater (Weston et al., 2006). The observed increase in CO_2 production, concomitant with no change in CH_4 production, affects the global warming potential of these wetlands. Previous studies have asserted that saltwater intrusion into wetlands increases CO_2 production and decreases CH_4 production, decreasing the net global warming potential of these wetlands (Chambers et al., 2011). However, in this case, CH_4 production rates remained constant with increases in salinity, whereas the CO_2 production rate accelerated, resulting in a net increase in the global warming potential of all three wetland soil types.

The effect of salinity treatments on DOC concentrations within the porewater was mediated by wetland soil type, as demonstrated by the opposing response of DOC in the cypress dome and the mineral marsh (an increase with salinity), compared with the bayhead swamp (a slight decrease with salinity). In the bayhead swamp, DOC was lost via export into the surrounding water in response to salinity, which was expected on the basis of previous findings that soils with a higher C content release more C in response to elevated salinity levels (Marton et al., 2012). However, concentrations of DOC in the surrounding water of the bayhead swamp showed no change with salinity, despite the substantial flux of DOC from the porewater. Flocculation is probably responsible for this discrepancy: on exposure to saline water, approximately 13% of the DOC within surface waters can immediately flocculate and shift to particulate organic matter (Ardón et al., 2016). In the mineral marsh and cypress dome, the increases in porewater DOC concentrations in response to salinity could be a result of the stimulation of organic matter mineralization (Weston et al., 2011; Chambers et al., 2014). In addition, average DOC within all the treatments decreased with time over the course of the 3-wk experiment, probably because of the effects of soil collection. Dissolved organic C has been observed to "leak" from wetland soil cores for several hours after coring because of the severing and death of roots, resulting in the observed decrease in labile DOC in the porewater over time (Gribsholt and Kristensen, 2002).

Nitrogen Dynamics

Ionic displacement resulting from an increase in salinity probably caused the desorption of NH_4^+ from the CEC in all of the wetland soil types, and the magnitude of this process increased with salinity. Previous research has demonstrated that exchangeable NH_4^+ is liberated from the soil particles within hours because of the elevated competition for exchange sites with monovalent and divalent cations from salinity increases (Seitzinger et al., 1991; Rysgaard et al., 1999; Gardner et al., 1991). However, no previous research has characterized the export of NH_4^+ from the porewater into the surrounding water in the short term within different wetland soil types. In this study, NH_4^+ concentrations increased in the porewater within 1 d of salinity exposure, and then peaked in the surrounding surface water within the first week of the study, though the concentration of liberated NH_4^+ differed by wetland soil type (supplemental data). The timescale of NH_4^+ exchange from the CEC is consistent with a similar studies that exposed wetland soils to

increased salinity treatments (Seitzinger et al., 1991; Weston et al., 2006, 2011; Jun et al., 2013; Ardón et al., 2013). The highest percentage of export under the 5-ppt treatment was in the bayhead swamp treatment (94.7%), which we attribute to the high organic matter content and the potential for organic N mineralization to NH_4^+. The 15-ppt treatment had a slightly reduced export of NH_4^+ out of the porewater (66–84%) but higher concentrations within the porewater, indicating that although more NH_4^+ was present, it was more tightly held within the soil. Extractable NH_4^+ increased between the 5-ppt and 15-ppt treatments, which can be attributed to increases in mineralization catalyzed by the availability of sulfate (Noe et al., 2013; Weston et al., 2006, 2011; Chambers et al., 2013; Ardón et al., 2016), as well as differences in liberation of NH_4^+ from the CEC between treatments (Rysgaard et al., 1999). Extractable NH_4^+ concentrations also differed among the wetland soil types, demonstrating the importance of inherent soil physiochemical properties in mediating the response of NH_4^+ availability to increased salinity.

Phosphorus Dynamics

Soluble reactive P concentrations in both the porewater and the surrounding water were highly dependent on wetland soil type. In the bayhead swamp, SRP concentrations decreased with increasing salinity, whereas the cypress dome and mineral marsh showed the opposite trend in the porewater. Almost all of the SRP produced in the porewater was exported into the surrounding water in the bayhead swamp (83–103%). The maximum occupation of exchange sites would result in excess SRP being readily exported into the surrounding water, as shown by the high percentage of export. In contrast, despite the mineral marsh and cypress dome having higher average concentrations of SRP in the porewater, the SRP appeared to be held in the porewater more tightly, with only 2 to 6% of the SRP within the porewater of the 15-ppt treatments being exported into the surrounding water. This discrepancy between the concentrations in the porewater and the concentrations in the surface water can be attributed to differences in soil type (Herbert et al., 2015). Both the mineral marsh and cypress dome contained more inorganic C than the bayhead swamp, and SRP exported from the porewater into the surrounding water could complex with inorganic C and form particulates that flocculate and are removed from the water column, and were therefore not detected as dissolved nutrients (Boström et al., 1988). In addition to abiotic factors such as soil type mediating SRP export into the surrounding water, the P cycle is tightly coupled with the cycling of both Fe and S, both of which are heavily influenced by pH changes produced by an influx of seawater (Portnoy and Giblin, 1997). Seawater can catalyze a concomitant increase in both pH and the concentrations of dissolved Al and Fe, which have the ability to complex with phosphate, thereby potentially altering P dynamics.

Experimental Design Considerations

We implemented a controlled laboratory experiment to isolate and quantify the changes in greenhouse gas production, MBC, and porewater and surrounding water nutrients in response to salinity. Although this approach successfully addressed the study objectives, consideration should be taken when extrapolating results directly to a field setting. For example, this study only focused on the soil system: plants were excluded from the experimental cores because the nature and magnitude of their influence could not be held constant across the experimental units. However, in the field, plants are expected to play a significant role in mediating nutrient availability and exchange between porewater and surrounding water pools (Bedford et al., 1999). Likewise, phytoplankton was removed from the added surface water through filtering prior to addition to the experimental cores. Despite these limitations, this study provides information on how different freshwater wetland soil types are expected to respond in the short term to increases in salinity, as well as the magnitude and timing of these responses. Future studies should test these conclusions under field conditions.

CONCLUSION

This study represents the first experimental attempt to quantify the movement of bioavailable nutrients (NH_4^+, SRP, and DOC) in different wetland soil types from the porewater of freshwater wetland soils to the surrounding water column following an increase in salinity. In general, the mineral-rich soils demonstrated a smaller response to saltwater intrusion than the more organic soils when it came to nutrient release and export, presumably caused by the differences in initial nutrient availability and how tightly those nutrients were held within the soil structure. Although this study only investigated short-term responses to saltwater intrusion (i.e., 3 wk), the finding will have important implications for coastal wetland systems exposed to periodic salinity pulses and demonstrates the vulnerability of coastal zones located near coastal peatlands to salinity-induced eutrophication.

SUPPLEMENTAL MATERIAL

The supplemental material contains a figure illustrating concentrations of both the porewater and surrounding water NH_4^+ over the course of the experiment. Each salinity treatment is averaged over wetland type, and showcases the increase in ammonium concentrations within the surrounding water by Day 7 of the experiment.

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