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RESEARCH ARTICLE

Saltwater and nutrient legacies reduce net ecosystem carbon storage despite freshwater restoration: insights from experimental wetlands

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Net ecosystem carbon balance is a comprehensive assessment of ecosystem function that can test restoration effectiveness. Coastal peatlands are globally important carbon sinks that are vulnerable to carbon loss with saltwater intrusion. It is uncertain how wetland carbon stocks and fluxes change during freshwater restoration following exposure to saltwater and elevated nutrients. We restored freshwater to sawgrass (*Cladium jamaicense*) peat monoliths from freshwater marshes of the Everglades (Florida, U.S.A.) that had previously been exposed to elevated salinity (approximately9 ppt) and phosphorus (P) loading (1 g P m^{-2} $year^{-1}$) in wetland mesocosms. We quantified changes in water and soil physicochemistry, plant and soil carbon and nutrient standing stocks, and net ecosystem productivity during restoration. Added freshwater immediately reduced porewater salinity from >8 to approximately 2 ppt, but elevated porewater dissolved organic carbon persisted. Above- and belowground biomass, leaf P concentrations, and instantaneous rates of gross ecosystem productivity (GEP) and ecosystem respiration (ER) remained elevated from prior added P. Modeled monthly GEP and ER were higher in marshes with saltwater and P legacies, resulting in negative net ecosystem productivities that were up to 12× lower than controls. Leaf litter breakdown rates and litter P concentrations were 2× higher in marshes with legacies of added saltwater and P. Legacies of saltwater and P on carbon loss persisted despite freshwater restoration, but recovery was greatest for freshwater marshes exposed to saltwater alone. Our results suggest that restoration in nutrient-limited freshwater wetlands exposed to saltwater intrusion and nutrient enrichment is a slow process.

Key words: biogeochemistry, carbon, Florida Coastal Everglades, Long Term Ecological Research, phosphorus, saltwater intrusion, sea-level rise, soil elevation

Implications for Practice

- Whether or not freshwater restoration can reverse impacts of saltwater intrusion in coastal ecosystems is a fundamental uncertainty.
- Legacies of elevated saltwater and nutrients can persist and impede ecosystem structure and net ecosystem carbon storage.
- Sustained freshwater restoration may be an essential management strategy needed to protect vulnerable coastal ecosystems exposed to sea-level rise and saltwater intrusion.

Introduction

As ecosystems undergo succession and development, they generally increase net ecosystem carbon storage (Chapin et al. 2006. However, disturbances can affect net ecosystem carbon storage and subsequently impact ecosystem development and resilience to environmental drivers (Kominoski et al. 2018; Gaiser et al. 2020). Sea-level rise is a global-scale disturbance that is rapidly increasing saltwater intrusion in coastal wetland ecosystems (Herbert et al. 2015; Tully et al. 2019). Low-lying coastal ecosystems become particularly vulnerable to saltwater intrusion, resulting in a shift in chemical and hydrological regimes (Herbert et al. 2015; Osland et al. 2016; Dessu et al. 2018). Coastal wetland ecosystems are important global carbon sinks that are directly threatened by climate change, land-use change,

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and interactions of both with saltwater intrusion from sea-level rise (Kirwan & Megonigal 2013; Tully et al. 2019). The fate of coastal ecosystems as sea-level rise and saltwater intrusion increase will be determined by the ability of these ecosystems to store carbon (Kominoski et al. 2018). Forecasting whether coastal ecosystems continue to develop, transition to another vegetated state, or slowly or abruptly decline to open water, requires a mechanistic understanding of how saltwater intrusion affects carbon production, storage, and export as sea levels rise (Morris et al. 2002; Jiang et al. 2012; Chambers et al. 2019).

The relative sensitivity of marsh plants to saltwater intrusion is species-specific and dependent on antecedent conditions and interacting stressors (Flynn et al. 1995; Breithaupt et al. 2020). Recent experimental manipulations of saltwater intrusion have revealed consistent declines in plant productivity (Herbert et al. 2018; Wilson et al. 2018, 2019; Solohin et al. 2020), declines in soil elevation and carbon storage (Charles et al. 2019; Solohin et al. 2020), and increases in soil organic matter breakdown (Charles et al. 2019; Servais et al. 2020). In addition, nutrient enrichment (elevated phosphorus [P]) stimulates sawgrass (*Cladium jamaicense*) above- and belowground biomass, regardless of the presence of saltwater (Charles et al. 2019; Wilson et al. 2019). Phosphorus enrichment also increases root productivity and leaf and root litter decomposition, regardless of the presence of saltwater (Charles et al. 2019; Servais et al. 2019). Compared to the subsidy effect of P, salinity increases osmotic stress and ionic concentrations (Herbert et al. 2015; Tully et al. 2019), which causes root mortality and soil elevation loss (Charles et al. 2019) and desorption of dissolved carbon and nutrients from peat soils (Servais et al. 2019; Wilson et al. 2019). Control wetlands, without added saltwater or P, had negligible changes in soil elevation during the study period (Charles et al. 2019). Carbon losses (e.g. leached dissolved organic carbon, increased microbial, and plant respiration) exceeded carbon production and retention (i.e. gains; e.g. primary production, root productivity, and aboveground biomass growth), resulting in consistent soil elevation declines with exposure to saltwater with and without added P (Table 1). This decrease in soil elevation (23 mm year^{-1}) is an order of magnitude higher than global (2.8 mm year^{-1}) and local (7.7 mm year^{-1}) estimates of sea-level rise (Watson et al. 2015; Dessu et al. 2018).

Declines in net ecosystem carbon storage are expected in freshwater peatlands exposed to saltwater intrusion without restored or increased freshwater. The Florida Everglades is the largest subtropical freshwater peatland in the United States that is being restored through reestablishment of historic freshwater flows (NASEM 2018; Sarker et al. 2020). More than a century of draining and building of canals has reduced the original size of the historic Everglades by half (McVoy 2011). These changes resulted in reductions of freshwater flows to the southern Everglades, making it increasingly vulnerable to saltwater intrusion (Davis & Ogden 1994). The Everglades is an extremely phosphorus-limited, upside-down estuary, whereby marine water pulses stimulate wetland productivity (Childers et al. 2006), but paradoxically freshwater and brackish marshes occupying the leading edge of saltwater intrusion are sensitive to elevated salinities (Charles et al. 2019; Wilson et al. 2019). Coupled with recent findings of persistent elevation loss in wetlands exposed to elevated salinity (Stagg et al. 2018; Charles et al. 2019; Solohin et al. 2020 and references therein), wetlands exposed to salinity and P may have strong internal feedbacks that reinforce a persistent degraded state (sensu Søndergaard et al. 2001; Suding et al. 2004). Freshwater pulses into brackish soils can decrease osmotic stress and promote methanogenesis (Chambers et al. 2013) by removing accumulated Cl^-, HS^-, and SO_4^{2-} (Jolly et al. 2008). Freshwater pulses decrease salinity and increase primary production in coastal swamp forests (Middleton et al. 2015). Freshwater restoration will need to maintain and enhance soil elevation gains and net ecosystem

Table 1. Summarized published results from a saltwater × phosphorus (P) manipulation study that quantified the responses of freshwater marshes to saltwater intrusion. Freshwater sawgrass (*Cladium jamaicense*) peat monoliths were exposed to freshwater (control, FW), elevated P (FWP), elevated saltwater (SW), and elevated saltwater and P (SWP) from 7 February 2015 to 12 February 2017. A dominant positive (+) or negative (−) effect is from a two-way ANOVA test. When both saltwater and P effects were found (i.e. either main or interactive effects), the stronger main effect was presented. Two-way ANOVA and Tukey's HSD post hoc comparison were used to determine a difference at a significance level of $\alpha = 0.05$. Superscripted letters represent results from Tukey's HSD test ($p < 0.05$). Tukey's HSD test was not performed on gross ecosystem productivity and ecosystem respiration. (SRP, soluble reactive phosphorus, DOC, dissolved organic carbon, ER, ecosystem respiration; GEP, gross ecosystem productivity).

Response variable	*FW*	*FWP*	*SW*	*SWP*	p	*Effect*	*Reference*
Porewater salinity (ppt)	0.46^{a}	0.44^{a}	8.3^{b}	8.0^{b}	<0.05	Salt (+)	Servais et al. (2019)
Porewater SRP (μmol L^{-1})	0.15^{a}	0.20^{a}	0.38^{b}	0.39^{b}	<0.001	Salt (+)	Wilson et al. (2019)
Porewater DOC (μmol L^{-1})	1862^{a}	1981^{a}	3281^{b}	3268^{b}	<0.001	Salt (+)	Wilson et al. (2019)
Porewater NH_4^+ (μmol L^{-1})	6.6^{a}	8.8^{a}	36.5^{b}	28.6^{b}	<0.001	Salt (+)	Wilson et al. (2019)
Sawgrass aboveground biomass (g C m^{-2})	294^{a}	846^{b}	398^{a}	627^{ab}	<0.01	Phosphorus (+)	Wilson et al. (2019)
Sawgrass root productivity (g C m^{-2} year^{-1})	81.3^{ab}	179.2^{a}	49.1^{b}	126.5^{ab}	<0.01	Phosphorus (+)	Charles et al. (2019)
Sawgrass leaf litter breakdown (k day^{-1})	0.0014^{a}	0.002^{b}	0.0015^{a}	0.002^{b}	<.001	Phosphorus (+)	Charles et al. (2019)
Sawgrass root (0–7.5 cm) breakdown (k day^{-1})	0.0009^{a}	0.0011^{b}	0.0008^{a}	0.0012^{b}	<0.01	Phosphorus (+)	Servais et al. (2019)
Sawgrass belowground biomass (g C m^{-2})	456^{a}	599^{b}	252^{c}	30^{c}	<0.05	Salt (−)	Charles et al. (2019)
Soil elevation change (cm year^{-1})	-0.04^{ab}	0.88^{a}	-2.75^{b}	-2.29^{b}	<0.001	Salt (−)	Charles et al. (2019)
GEP (μmol C m^{-2} s^{-1})	6.6^{a}	15.8^{b}	7.4^{a}	12.3^{b}	<.001	Phosphorus (+)	Wilson et al. (2019)
ER (μmol C m^{-2} s^{-1})	1.4^{a}	3.2^{b}	1.4^{a}	2.7^{b}	<.001	Phosphorus (+)	Wilson et al. (2019)

carbon storage to promote development trajectories in coastal ecosystems (Nyman et al. 2006; Neubauer 2008).

Our objective was to test whether freshwater restoration, aimed at remediating the effects of saltwater and P legacies, could reestablish wetland ecosystem development trajectories that increase net ecosystem carbon storage. We used sawgrass-peat monoliths collected from freshwater wetlands that were inundated with brackish water (approximately 9 ppt) and enriched with P (1 g P m^{-2} $year^{-1}$) during the manipulation experiment preceding our restoration experiment. We tested the following questions: (1) Can restoring freshwater to freshwater sawgrass marshes offset legacies of elevated saltwater and P?, (2) What biogeochemical mechanisms are altered by freshwater restoration?, and (3) Can freshwater restoration enhance net ecosystem carbon storage and transform wetlands exposed to elevated saltwater and nutrients from carbon sources to carbon sinks?

Methods

Experimental Design

We used sawgrass-peat monoliths placed in polycarbonate boxes (3,500 cm^2 surface area × 53 cm height) in an outdoor mesocosm facility at Florida Bay Interagency Science Center, Key Largo, Florida (Fig. 1). In July 2014, intact plant–soil monoliths were transported from a nutrient-unenriched freshwater marsh wetland in the Everglades to the facility. The monoliths were inundated under the freshwater condition to allow acclimation for 7 months; an augmentation of seawater and P was initiated on 7 February 2015 and maintained until 12 February 2017 to quantify responses to long-term exposure to elevated saltwater and P. Details on collection site characteristics, material handling, acclimation, incubation, and manipulation are provided elsewhere (Charles et al. 2019; Servais et al. 2019; Wilson et al. 2019). Briefly, freshwater was collected from the C-111 Canal (25°17′31.74″N, 80°27′21.59″W). Saltwater was pumped directly from Florida Bay. Freshwater and diluted seawater (salinity: approximately 9 ppt) were added manually 2–3 times per week to keep surface soils inundated. Phosphoric acid (0.45 mg P day^{-1}) was pumped directly into the P-added plots. The manipulation experiment lasted for 24 months and included a total of 24 experimental plots, including the control ($n = 6$) and three legacy treatments ($n = 6$ per treatment): (i) freshwater (the control or FW), (ii) freshwater and added P (FWP_L), (iii) added saltwater (SW_L), and (iv) added saltwater and P (SWP_L).

Immediately following the manipulation experiment, we drained, rinsed, and refilled all holding containers with freshwater. Freshwater was manually added to each container three times per week from 12 February 2017 to 19 June 2018, maintaining water depth above the soil surface at approximately 10 cm.

Surface and Porewater Physicochemistry

Physicochemical conditions were monitored ($n = 6$ replicates per legacy treatment) monthly at surface water and porewater. A porewater sipper with an aquarium air stone (4 cm long × 1 cm diameter) was inserted to 15 cm depth near the middle of each monolith prior to the manipulation experiment. Sulfide concentration in porewater (HS^-; $n = 3$ per legacy treatment) was measured until not detected (2 March, 3 July, and 1 August 2017). Salinity, conductivity, and temperature were surveyed with a YSI Model 600 XL (Xylem, Inc., Yellow Springs, OH, U.S.A). Water samples were collected using a 60-mL syringe, filtered through a 0.7-µm glass fiber filter, and stored at −20°C until analysis. Water chemistry was analyzed at the Southeast Environmental Research Center Nutrient Analysis Laboratory (SERC-NAL). SERC-NAL followed internal and external quality assurance practices and is NELAC certified for non-potable water-General Chemistry under State Lab ID E76930. Filtered

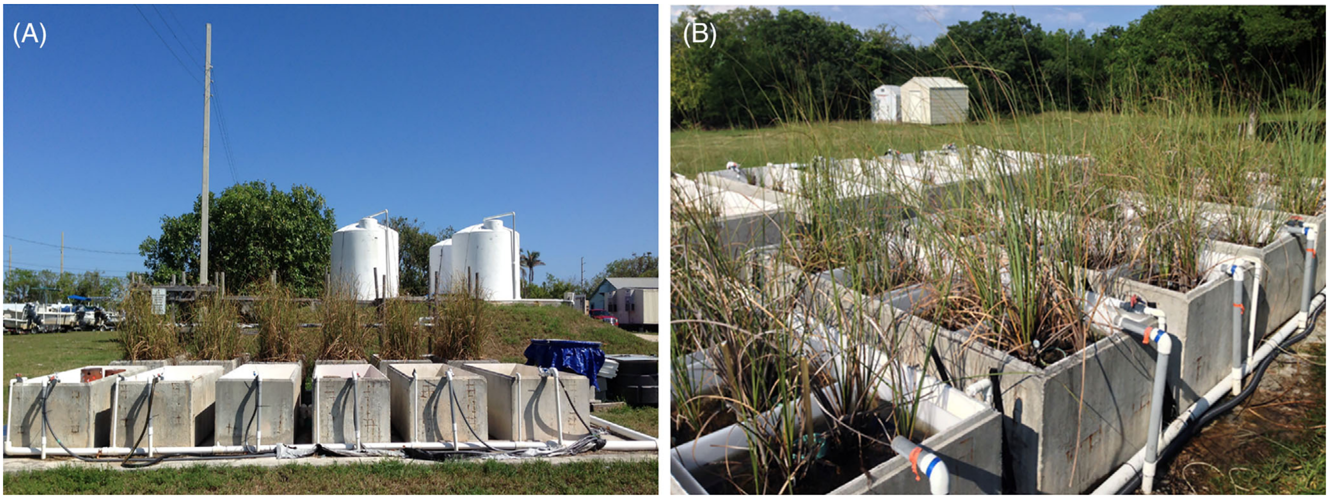

Figure 1. Experimental wetland mesocosm facility, key largo, Florida, U.S.A. (A) Image illustrates the overall footprint of the facility with raised water headtanks in the background and concrete basins with and without wetland soils and sawgrass (*Cladium jamaicense*) plants in the foreground. (B) Image illustrates how experimental sawgrass (*Cladium jamaicense*) wetland mesocosms were in closed-bottom, self-contained polycarbonate bins that enabled replication within and among treatments.

samples were analyzed for dissolved organic carbon (DOC), ammonium (NH_4^+), soluble reactive phosphorus (SRP), and HS^-. The concentration of SRP was analyzed on an Alpkem RFA 300 autoanalyzer (OI Analytical, College Station, TX, U.S.A.), and DOC (and total organic carbon [TOC]) was analyzed with a Shimadzu 5,000 TOC Analyzer (Shimadzu Corporation, Columbia, MD, U.S.A.). Porewater HS^- concentrations were quantified following standard methods (McKee et al. 1988). The concentration of total phosphorus (TP) was analyzed using the high-temperature persulfate digestion method (Solórzano & Sharp 1980).

Organic Carbon Flux and Elemental Concentrations

Sawgrass aboveground biomass was measured in February, May, and July of 2017 and February, April, and June of 2018 using a non-destructive allometric method (Daoust & Childers 1998). The decomposition of sawgrass litter was calculated from mass loss and expressed as a first-order decay constant (Davis 1991). Standing dead *Cladium jamaicense* leaf litter was removed from plants from all mesocosms. Litter was oven-dried at 40°C for 1 week and placed into 1-mm mesh bags ($n = 2$ per replicate mesocosm per sampling event). Litter bags were incubated on surface soils within each mesocosm beginning 11 April 2017 for 155 and 317 days. Collected sample bags were immediately placed on ice and returned to the lab. Incubated litter was rinsed with deionized water, oven-dried at 60°C until mass stabilized, and subsequently weighed for individual mass remaining. A decay constant, k (day^{-1}), was calculated over sampling intervals as a first-order decay constant using the following:

$$y = e^{-\text{kt}}$$

where y is the proportion of mass remaining at time t.

After completion of the freshwater restoration manipulation, samples for C, N, and P content were collected for live sawgrass leaf, live fine root, and soil ($n = 6$ replicates per legacy treatment). The live sawgrass leaf and root were identified based on color and texture grown from short shoots (<40 cm). We cut soil cores into a rectangular cuboid ($56\ \text{cm}^2$ surface area × 25 cm height). Biomass and soil samples were oven-dried at 60°C until mass stabilized. Dried samples were ground using a ball mill (8000-D, Spex SamplePrep, Metuchen, New Jersey, U.S.A.) and subsequently analyzed for C and N content using a CHN Analyzer (Carlo Erba 1,500, Milan, Italy) and P content using the ash/acid extraction method followed by the ascorbic acid method for spectrophotometric analysis (Solórzano & Sharp 1980). Soil bulk density was determined by dividing dry weight by core volume.

Ecosystem Metabolism

Monthly CO_2 fluxes were measured ($n = 4$ replicates per legacy treatment) around midday (approximately 10:00 to approximately 15:00) from May 2017 to June 2018. We used transparent polycarbonate chambers consisting of a bottom collar, the main chamber ($0.2\ \text{m}^2$ × 120 cm height), and a top lid ($0.2\ \text{m}^2$ × 30 cm height). We manipulated multiple levels of photosynthetically active radiation (PAR) to mimic diel changes in PAR by shading chambers with different layers of plastic mesh. Gas samples were measured on a CO_2/H_2O analyzer (LI-840A, LI-COR Biosciences, Lincoln, NE, U.S.A.). Net ecosystem productivity (NEP) was calculated as the linear slope of CO_2 concentration over time for the 30–100% light levels, and ecosystem respiration (ER) was calculated as the slope of CO_2 concentration under the dark condition (assumed to be similar to nighttime ER). Gross ecosystem productivity (GEP) was estimated by summing NEP and ER. We used nonlinear least square models for fitting monthly CO_2 fluxes with environmental variables. Briefly, we fitted hyperbolic relationships between GEP and PAR, and exponential relationships between ER and temperature per plot on each sampling event. Fluxes of GEP and ER were modeled at a 15-min frequency by using the empirically derived parameters and climatic data (PAR, temperature). See Supplement S1 for additional details.

Statistical Analyses

All statistical analyses were conducted using R v.1.0.143 (Core Team 2017). Differences in water physicochemistry, aboveground biomass, and short-term carbon flux rate among legacy treatments were tested through linear mixed-effects models using the R package "nlme" (Pinheiro et al. 2018). The model was to determine the main effect of saltwater legacy, P legacy, time (sampling date), and their interactions with a random effect of plot number. When an interactive effect of saltwater legacy and date was detected, a pairwise comparison within each sampling event was assessed with a least-squares ANOVA using the "lsmeans" package (Lenth 2018) to identify the effectiveness of the saltwater legacy treatments (i.e. SW_L, SWP_L) and the P legacy treatments (i.e. FWP_L, SWP_L) within sampling dates. Legacy effects on the overall mean of belowground biomass, soil bulk density, leaf litter breakdown, modeled carbon flux, and carbon and nutrient content were determined using a two-way ANOVA. We then assessed mean differences among the control and legacy treatments using a least-square means multiple comparison test adjusted to Tukey's HSD. Log-transformed variables were used for meeting the normality of residuals and the homogeneity of variances using visual inspection with a normal probability plot. The critical level of significance was set at $\alpha = 0.05$.

Mann–Kendall and Theil–Sen slope tests were employed to assess trajectories of physicochemical conditions, aboveground biomass, and short-term carbon flux. All values were analyzed without data transformation because the non-parametric methods have advantages of no strict rules required for residuals with non-normality, time-series data with serial dependence, and missing data (Sen 1968; Hirsch & Slack 1984; Theil 1992). We applied the Mann–Kendall test of the null hypothesis that there is no monotonic trend at a significance level of 0.05. When the null hypothesis was rejected ($p < 0.05$), a slope of an existing monotonic trend was estimated with the Theil–Sen slope. The modified Mann–Kendall test determined the statistical significance of the Theil–Sen slope after accounting for serial autocorrelation using the R packages "Kendall" (McLeod 2015) and "fume" (Santander Meteorology Group 2012). The slope of lines over a pair of all available data points was calculated as the median of all possible pairwise slopes between each and another monthly data. To ease the comparison among legacy treatments, we provided a percent change (% change year^{-1}) from a mean of sample data over the observation period (Yue & Hashino 2003).

Differences in modeled ecosystem metabolism were determined using pairwise comparison. Modeled metabolism outputs were subtracted between the FW and other legacy treatments (e.g. $\Delta\text{GPP}_{(n\,=\,1\text{–}1{,}000,\text{FW-FWP})} = \text{GPP}_{(n\,=\,1\text{–}1{,}000,\text{FW})} - \text{GPP}_{(n\,=\,1\text{–}1{,}000,\text{FWP})}$) for all combinations (i.e. FW versus FWP_L, SW_L, and SWP_L). The differences were either positive or negative values with the mean of zero if the modeled metabolism in the FW and legacy treatment plots were very similar. Statistical difference was defined when zero lies above or below 2.5% of a probability distribution (i.e. a significance level of 0.05). This approach is conceptually straightforward and avoids a strict assumption of normal distribution in other parametric tests and has been frequently used to find differences in resampling methods (Crowley 1992; Neubauer 2013).

Results

Surface and Porewater Chemistries

Adding freshwater reduced salinities from 9.2 to 2.8 ppt in porewater and from 8.5 to 2.9 ppt in surface water in SW_L and SWP_L (Fig. 2, Table 2). Salinities were maintained at low brackish levels (approximately 2.8 ppt) until September 2017, when Hurricane Irma's rainfall further decreased salinity by approximately 55% in the saltwater legacy plots. A long-term decline in salinity was observed in the SW_L (approximately −5% year^{-1}) (Table 2). Added freshwater rapidly reduced porewater HS^- concentrations from 0.22 mmol L^{-1} in the SW_L and 0.12 mmol L^{-1} in the SWP_L within the first 2 months (Table 2).

Porewater NH_4^+ concentrations were higher in the SW_L than in the FWP_L (ANOVA, $F_{1,21} = 8.1, p < 0.01$) and P legacies (ANOVA, $F_{1,21} = 8.9$, $p < 0.01$) (Table 2). Higher porewater NH_4^+ concentrations were observed in SW_L and SWP_L than FW from June to October 2017 due to the saltwater legacy (Table 2). In contrast, the P legacy decreased porewater NH_4^+ concentrations from June to December 2017 (Table 2), suggesting biotic uptake during the wet growing season. When the saltwater and P legacies coexisted (i.e. SWP_L), the effect of P legacy not only offset the saltwater legacy but also had a lasting impact, as NH_4^+ concentrations declined over the study period in the SWP_L (Table 2). Similar to saltwater legacy effects on porewater NH_4^+ concentrations, porewater DOC concentrations were higher and varied over time in SW_L and SWP_L due to an interactive effect of saltwater legacy and time (ANOVA, $F_{14,293} = 2.4$, $p < 0.01$) (Fig. 2, Table 2).

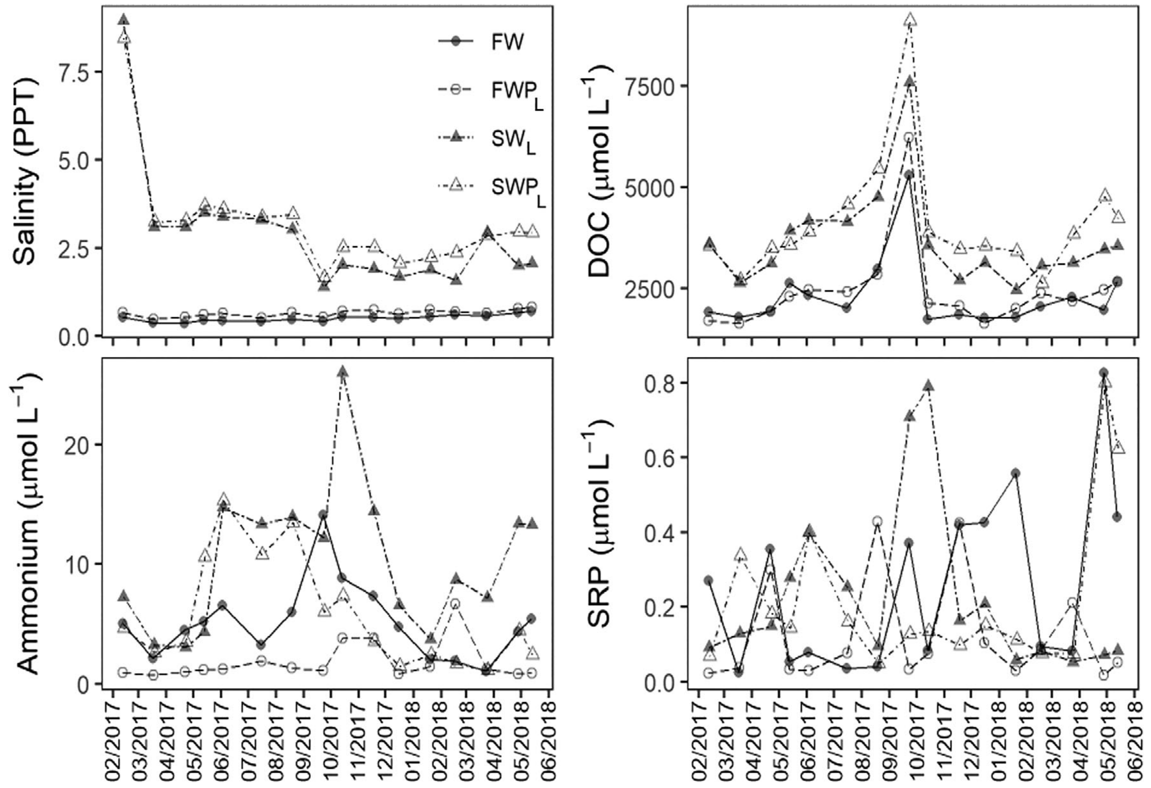

Figure 2. Changes in porewater physicochemistry during freshwater restoration of freshwater sawgrass (*Cladium jamaicense*) peat wetland mesocosms from freshwater (control, FW), and legacy elevated saltwater and phosphorus (P) treatments [elevated P (FWP_L), elevated saltwater (SW_L), and elevated saltwater and P (SWP_L)]. Error bars are omitted for clarity.

Table 2. Mean and standard error of physicochemical variables ($n = 6$ per treatment), biomass ($n = 6$ per treatment), and short-term metabolism ($n = 4$ per treatment) during freshwater restoration of freshwater sawgrass (*Cladium jamaicense*) peat wetland mesocosms from freshwater (control, FW), and legacy elevated saltwater and phosphorus (P) treatments [elevated P (FWP_L), elevated saltwater (SW_L), and elevated saltwater and P (SWP_L)]. A temporal trend (%-change year^{-1}) was estimated using the Mann–Kendall (MK) and Theil–Sen (T–S) slope tests. A trend (i.e. slope coefficient) can be interpreted as a percent change from the overall average. Bolded trends represent an increase (+) or decrease (−) at a significance level of $p < 0.05$. No trend analysis was conducted for HS^- concentration, belowground biomass, bulk density, and leaf litter breakdown. Superscripted letters and bolded values represent increases ($p < 0.05$) among control and legacy treatment responses using two-way ANOVA and Tukey's HSD. (TP: Total phosphorus).

	FW			*FWP$_L$*			*SW$_L$*			*SWP$_L$*		
	Mean	*T-S*	*MK*	*Mean*	*T-S*	*MK*	*Mean*	*T-S*	*MK*	*Mean*	*T-S*	*MK*
Surface water												
Salinity (ppt)	0.54 ± 0.01^{a}	**5.3**	<0.001	0.63 ± 0.02^{a}	4.2	<0.001	**2.2 ± 0.1^{b}**	**−5.1**	0.01	**2.5 ± 0.07^{b}**	−2.2	0.15
Conductivity (S cm^{-1})	0.98 ± 0.02^{a}	**4.6**	<0.001	1.1 ± 0.03^{a}	3.9	<0.001	**8.6 ± 0.4^{b}**	**−5**	<0.01	**8.7 ± 0.4^{b}**	−2	0.14
DOC (μM)	1800 ± 50	**2**	0.01	1800 ± 50	1.6	0.08	2,100 ± 80	−3.4	0.14	2,300 ± 70	−1.7	0.43
NH_4^+ (μM)	1.7 ± 0.3	5.1	0.08	2.4 ± 0.4	−3.1	0.76	3.6 ± 0.8	5.7	0.43	1.4 ± 0.07	−4.3	0.07
SRP (μM)	0.23 ± 0.05	**9.5**	0.01	0.22 ± 0.04	4.1	0.42	0.1 ± 0.01	2.9	0.69	0.095 ± 0.02	**−6.6**	0.04
TP (μM)	1.2 ± 0.1	1.1	0.20	0.97 ± 0.06	−7.7	0.07	0.73 ± 0.05	1.8	0.62	1.1 ± 0.05	−3.7	0.20
Porewater												
Salinity (ppt)	0.51 ± 0.01^{a}	**4.7**	<0.001	0.65 ± 0.02^{a}	**2.9**	<0.01	**2.5 ± 0.1^{b}**	**−5.7**	0.02	**2.8 ± 0.1^{b}**	**−2.8**	0.34
Conductivity (S cm^{-1})	1.0 ± 0.06^{a}	**4.3**	<0.001	1.2 ± 0.03^{a}	**2.9**	<0.01	**9.1 ± 0.5^{b}**	−6.3	0.17	**9.3 ± 0.4^{b}**	**−2.6**	0.31
DOC (μM)	$2{,}300 \pm 100^{a}$	−0.1	0.69	$2{,}500 \pm 100^{a}$	0.7	0.06	**$3{,}700 \pm 200^{b}$**	−1.3	0.79	**$4{,}200 \pm 300^{b}$**	0.2	0.72
NH_4^+ (μM)	5.1 ± 0.6^{ab}	−4.5	0.55	1.9 ± 0.5^{a}	1.3	0.55	**11 ± 2^{b}**	1.9	0.49	5.8 ± 1^{ab}	**−14**	0.04
SRP (μM)	0.25 ± 0.05	**8.2**	<0.01	0.13 ± 0.03	−0.4	0.82	0.24 ± 0.05	−6.3	0.09	0.23 ± 0.06	−3.7	0.37
HS^- (mM)	0.01 ± 0.001^{a}	**—**	—	0.005 ± 0.001^{a}	—	—	0.22 ± 0.04^{b}	—	—	0.12 ± 0.01^{b}	—	—
Aboveground biomass (g C m^{-2})	296 ± 52.4^{a}	8.6	0.13	**868 ± 123^{bc}**	10.5	0.45	467 ± 56.6^{ac}	8.4	0.26	**$1{,}421 \pm 128^{b}$**	**23.6**	0.02
Belowground biomass (g C m^{-2})	$1{,}492 \pm 146^{a}$	—	—	**$2{,}226 \pm 231^{b}$**	—	—	1881 ± 136^{ab}	—	—	**2096 ± 165^{b}**	—	—
Soil bulk density (g C cm^{-3})	0.14 ± 0.01	—	—	0.14 ± 0.01	—	—	0.17 ± 0.01	—	—	0.18 ± 0.01	—	—
Leaf litter breakdown (k day^{-1})	0.001 ± 0.0004^{a}	—	—	0.0011 ± 0.0003^{a}	—	—	0.0017 ± 0.004^{ab}	—	—	**0.0026 ± 0.0005^{b}**	—	—
GEP(μmol C m^{-2} s^{-1})	7.53 ± 0.43^{a}	−0.3	0.55	**20.1 ± 0.66^{b}**	−0.2	0.38	11.6 ± 0.52^{a}	−0.8	0.26	**21.0 ± 0.76^{b}**	**0.6**	0.09
ER (μmol C m^{-2} s^{-1})	2.28 ± 0.15^{a}	0.5	0.38	**7.47 ± 0.26^{b}**	0	0.92	4.30 ± 0.17^{a}	0.3	0.52	**9.28 ± 0.38^{b}**	**0.9**	<0.01

Surface water and porewater SRP were not different among legacy treatments (Table 2). In all legacy treatments, there were no temporal trends in SRP concentrations in porewater; however, there was a decline in SRP concentrations in surface water in the SWP$_L$ (Table 2). Hurricane Irma caused rapid increases in porewater DOC concentrations in all control and legacy treatments; whereas hurricane-induced increases in pore NH$_4^+$ and SRP concentrations were only observed in the SW$_L$.

Above- and belowground Biomass and Elemental Concentrations

The SW$_L$ had increased aboveground growth in the last 6 months (from February to June 2018) of freshwater restoration (LSMEANS, $p < 0.05$). An interactive effect of saltwater legacy and date (ANOVA, $F_{5,105} = 3.16, p < 0.05$) indicated a shift of saltwater legacy effect over time. The main effect of P legacy (ANOVA, $F_{1,21} = 33.6$, $p < 0.001$) remained effective throughout the study. Aboveground biomass was lower in FWP$_L$ than SWP$_L$, and aboveground biomass increased in SWP$_L$ but not in FWP$_L$ wetlands (Table 2). A shift of saltwater legacy observed in aboveground biomass was also observed for belowground biomass. During freshwater restoration, the P legacy (ANOVA, $F_{1,21} = 7.8$, $p < 0.05$) resulted in the highest belowground biomass in FWP$_L$ followed, in order of decreasing biomass, by SWP$_L$, SW$_L$, and FW (Table 2).

Carbon concentrations did not vary in sawgrass leaf and fine root among legacy treatments, whereas nutrient concentrations varied due to legacy effects of salt and P (Table 3). Different legacies affected nitrogen concentrations in sawgrass leaf (saltwater legacy, ANOVA, $F_{1,21} = 5.37$, $p < 0.05$) and root (P legacy, ANOVA, $F_{1,21} = 5.30$, $p < 0.05$). Regardless of the differing legacies, nitrogen concentrations in leaf and root were lowered in all legacy treatments relative to FW (Table 3). Although P concentrations in root did not vary among legacy treatments, P concentrations were lowered in all legacy treatments relative to FW (Table 3). By contrast, leaf P concentrations were highest in FWP$_L$ and not different among the other legacy treatments or FW (Table 3). There were no interactive effects between the saltwater and P legacies (ANOVA, $F_{1,20} = 0.68, p > 0.05$) on leaf P contents; however, the saltwater legacy (ANOVA, $F_{1,21} = 11.0$, $p < 0.01$) decreased and the P legacy (ANOVA, $F_{1,21} = 9.7$, $p < 0.01$) increased leaf P contents. As a result of the opposite effects of the legacies, nutrient use efficiency of sawgrass leaf, calculated as a molar ratio of C to P content, was the highest in SW$_L$ (7454) followed by SWP$_L$ (6693), FW (6512), and FWP$_L$ (4995), implying higher efficiency for the use of carbon and P in saltwater legacy plots than the freshwater plots.

Leaf Litter Breakdown and Elemental Concentrations

The highest litter k occurred in SWP$_L$ and was approximately twice that of FW and FWP$_L$, whereas the intermediate breakdown rate in SW$_L$ was not different from any other plots (Table 2). Litter breakdown rates were higher in the saltwater legacy than in the freshwater plots (ANOVA, $F_{1,21} = 8.89$, $p < 0.01$), where the P and interactive P and saltwater legacies were absent.

After the 305 days of incubation, carbon and nitrogen concentrations in sawgrass leaf litter did not vary among legacy treatments; however, leaf litter P concentrations were the highest in SWP$_L$ followed by FWP$_L$, FW, and SW$_L$ due to the P legacy (ANOVA, $F_{1,21} = 16.7, p < 0.001$) (Table 3). Phosphorus concentrations were approximately 2× higher in live sawgrass leaf than leaf litter in FW, as well as FWP$_L$ and SW$_L$, whereas P concentrations were similar between the live leaves and leaf litter in the SWP$_L$ (Table 3).

Soil Elemental Concentrations

The saltwater legacy (ANOVA, $F_{1,21} = 9.4, p < 0.01$) increased soil bulk density by 25% in the saltwater legacy treatments;

Table 3. Mean ($n = 6$ per treatment) and standard error of carbon (C), nitrogen (N), and P content in sawgrass (*Cladium jamaicense*) leaves, sawgrass leaf litter, soil, and sawgrass roots during freshwater restoration of freshwater sawgrass (*C. jamaicense*) peat wetland mesocosms from freshwater (control, FW), and legacy elevated saltwater and phosphorus (P) treatments [elevated P (FWP$_L$), elevated saltwater (SW$_L$), and elevated saltwater and P (SWP$_L$)]. The live samples were collected on the last day (01 June 2018) of the experiment, while the leaf litter samples were collected upon the termination of litter decomposition experiment (305th day, 12 February 2018). Superscripted letters and **bolded** values represent significant differences ($p < 0.05$) among control and legacy treatment responses using two-way ANOVA and Tukey's HSD.

	FW	*FWP$_L$*	*SW$_L$*	*SWP$_L$*
Sawgrass leaf				
C (mg g^{-1})	438 ± 4.9	439 ± 4.8	431 ± 8.2	448 ± 7.3
N (mg g^{-1})	**6.6 ± 0.5^{a}**	5.9 ± 0.5^{ab}	5.7 ± 0.2^{ab}	**4.9 ± 0.3^{b}**
P (μg g^{-1})	**179 ± 11^{a}**	**230 ± 13^{b}**	**151 ± 8.8^{a}**	**176 ± 28^{a}**
Sawgrass leaf litter				
C (mg g^{-1})	474 ± 4.6	488 ± 12	485 ± 8.3	474 ± 7.6
N (mg g^{-1})	6.2 ± 0.4	6.1 ± 0.6	6.9 ± 0.4	6.9 ± 0.3
P (μg g^{-1})	**78.8 ± 13^{a}**	145 ± 15^{ab}	**76.4 ± 6.6^{a}**	**192 ± 55^{b}**
Soil				
C (mg g^{-1})	453 ± 6.9	462 ± 7.8	437 ± 6.9	431 ± 5.6
N (mg g^{-1})	26 ± 0.9	26 ± 1	27 ± 0.6	26 ± 0.8
P (μg g^{-1})	456 ± 26	455 ± 32	430 ± 21	543 ± 57
Sawgrass root				
C (mg g^{-1})	860 ± 78	965 ± 12	942 ± 11	931 ± 3.6
N (mg g^{-1})	**6.5 ± 0.59^{a}**	5.6 ± 0.52^{ab}	5.6 ± 0.22^{ab}	**4.4 ± 0.48^{b}**
P (μg g^{-1})	185 ± 25	178 ± 11	158 ± 25	134 ± 6.7

however, there were no differences in bulk density among legacy treatments (Table 2). Soil carbon, nitrogen, and P concentrations did not vary among control and legacy treatments (Table 3).

Instantaneous Ecosystem Metabolism

There were a total of 13 gas flux measurements in 16 subsampled plots ($n = 4$ per legacy treatment) per event except during overcast days (the number of plots per event [n] = 16 for 7 months, $n = 15$ for 3 months, $n = 12$ for 2 months, $n = 8$ for 1 month). Overall, average monthly GEP rates ranged from 6.3 ± 0.81 (standard error) μmol m^{-2} s^{-1}, measured in FW in June 2017, to 24.5 ± 5.7 μmol m^{-2} s^{-1}, measured in SWP_L in November 2017 (Table 2). The P legacy (ANOVA, $F_{1,13} = 39.8, p < 0.001$) resulted in higher short-term GEP rates in FWP_L and SWP_L than FW and SW_L, whereas the saltwater legacy had no effect on GEP (ANOVA, $F_{1,13} = 2.5$, $p > 0.05$) (Table 2).

The use of temperature-derived ER was not feasible because a logarithmic scale of ER rates was not correlated with air temperature in any plots ($n = 15$, $R^2 < 0.21$, $p > 0.05$) except for one FWP_L plot ($R^2 = 0.73, p < 0.01$). We assumed constant respiration rates in each month for all plots except for one FWP_L plot where the air temperature adjusted short-term ER rates. Overall, average monthly ER rates ranged from 1.4 ± 0.29 μmol m^{-2} s^{-1},

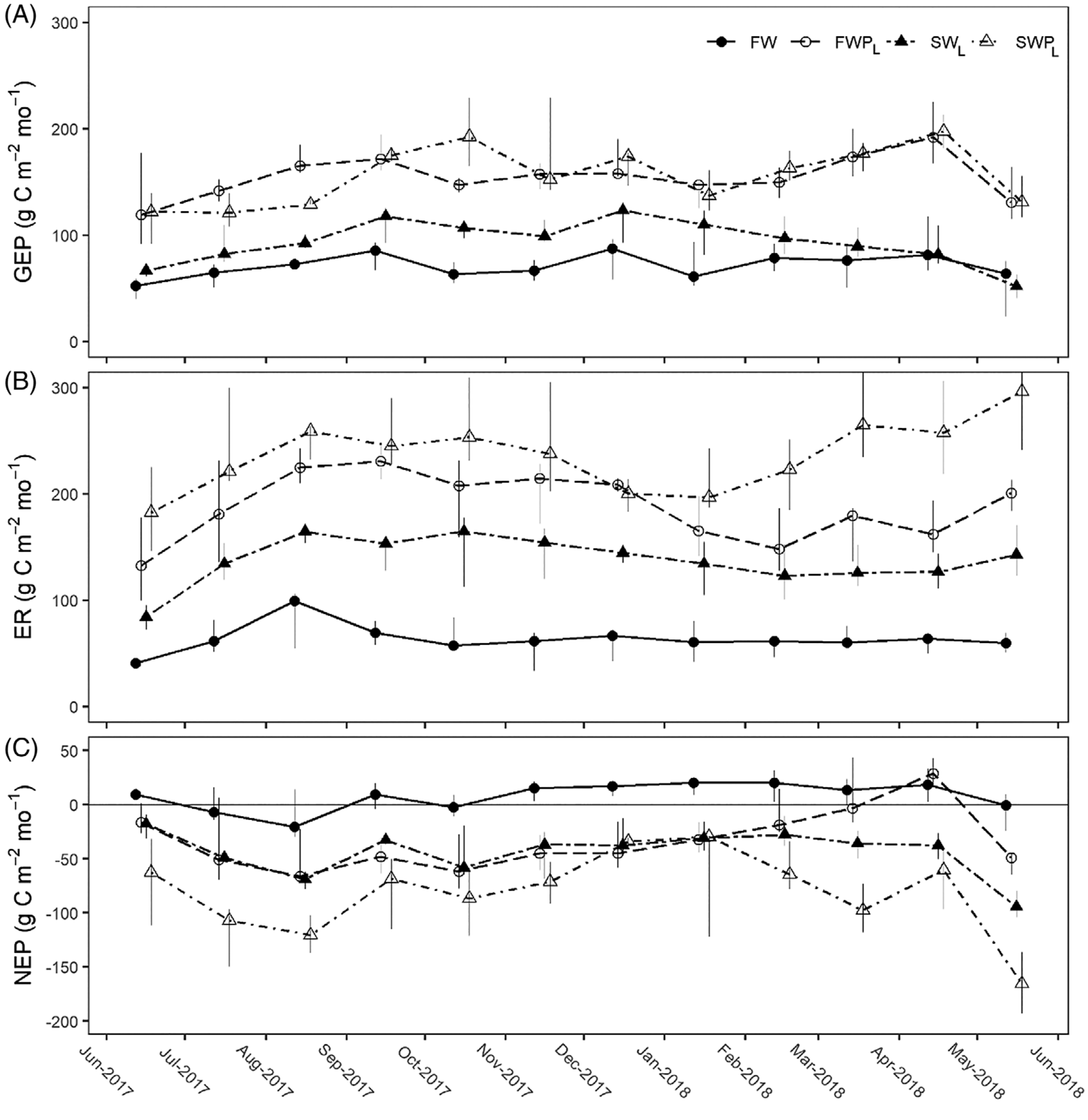

Figure 3. Values of modeled (A) gross ecosystem productivity (GEP) at maximum light levels, (B) ecosystem respiration (ER), and (C) net ecosystem productivity (NEP) during freshwater restoration of freshwater sawgrass (*Cladium jamaicense*) peat wetland mesocosms from freshwater (control, FW), and legacy elevated saltwater and phosphorus (P) treatments [elevated P (FWP_L), elevated saltwater (SW_L), and elevated saltwater and P (SWP_L)]. Points are medians, and error bars are 25th and 75th percentiles of 1,000 model outputs.

measured in SW_L in May 2017, to 12 ± 1.3 μmol m^{-2} s^{-1}, measured in SWP_L in June 2018 (data not shown). Both the P legacy (ANOVA, $F_{1,13} = 67.3$, $p < 0.001$) and saltwater legacy (ANOVA, $F_{1,13} = 11.4$, $p < 0.01$) stimulated short-term ER rates with higher rates in FWP_L and SWP_L than FW and SW_L (Table 2). A steady increase in short-term ER rates (Mann–Kendall, $p < 0.01$) was observed in SWP_L (Table 2).

Modeled Ecosystem Metabolism

There were differences in monthly modeled (see Supplement S1 for details) GEP rates in FWP_L and SWP_L compared to FW (Fig. 3A). These differences are not surprising, given that the P legacy plots had higher aboveground biomass (Table 2). Monthly modeled GEP rates in SW_L differed ($p < 0.05$) from FW only in 2 months during the wet season. Overall, there were effects of P legacy (ANOVA, $F_{1,34} = 269$, $p < 0.001$) and saltwater legacy (ANOVA, $F_{1,34} = 10.8$, $p < 0.01$) on modeled GEP rates. The P legacy approximately doubled modeled GEP rates in FWP_L compared to FW, whereas the saltwater legacy resulted in approximately 30% higher modeled GEP rates in SW_L than FW (Fig. 3(A)). Yet the P legacy effect appeared to offset the saltwater legacy when the two legacies coexisted, as modeled GEP rates in SWP_L and FWP_L were similar (Fig. 3(A)).

Modeled ER rates were different between the control and all legacy treatments with the highest rate in the SWP_L followed by FWP_L, SW_L, and FW (Fig. 3(B)). The saltwater legacy (ANOVA, $F_{1,34} = 24.7$, $p < 0.001$) approximately doubled the average modeled ER rate in SW_L compared to FW. The P legacy (ANOVA, $F_{1,34} = 454$, $p < 0.001$) approximately tripled the average modeled ER rate in FWP_L compared to FW. In contrast to the negligible saltwater legacy with P legacy on modeled GEP, the combined saltwater and P legacies (ANOVA, $F_{1,33} = 28.4$, $p < 0.001$) approximately quadrupled the average modeled ER rate in SWP_L compared to FW.

Higher modeled GEP than ER rates in FW resulted in net autotrophy, indicating that the system was a net sink of carbon annually (Fig. 3C). In contrast, all other legacy treatments were a net source of carbon (i.e. net heterotrophy). The P legacy (ANOVA, $F_{1,34} = 26.7$, $p < 0.001$) and the saltwater legacy (ANOVA, $F_{1,34} = 5.41$, $p < 0.05$) resulted in a similar magnitude of net heterotrophy (i.e. a system was releasing more carbon than it was retaining) in FWP_L and SW_L (Fig. 3C). There were no interactive effects between the saltwater and the P legacies (ANOVA, $F_{1,33} = 1.4$, $p > 0.05$); however, the additive effect of saltwater and P legacies reduced modeled NEP rates in SWP_L compared to FWP_L and SW_L by nearly 2× (Fig. 3C).

Discussion

Our results demonstrate saltwater and P legacies persisted following a continuous exposure (approximately 2 years) to saltwater, despite freshwater reintroduction (approximately 1 year), and maintained a net carbon release that would delay the recovery of net ecosystem carbon storage. The severity and duration of exposure to elevated saltwater and P preceding our freshwater restoration manipulation impacted the recovery of ecosystem processes, resulting in a carbon imbalance in the saltwater-exposed plots. We observed P legacies, continuously stimulating biotic growth and litter breakdown processes during freshwater restoration. Some plant responses recovered from prior saltwater exposure, especially when saltwater and P co-occurred. Notably, sawgrass root biomass increased the most during freshwater restoration in wetlands with a saltwater legacy. A reduction in salt stress, likely lowering ionic strength and toxicity, restored sawgrass above- and belowground biomass with a lag of approximately one year. Increased carbon and nitrogen availability also enhanced microbial SRP uptake and decomposition of plant litter, especially in the sediment–water interface, where enhanced nutrient recycling would supply emergent plant growth. However, this positive feedback mechanism disrupted the ecosystem carbon balance due to a net increase in autotrophic and heterotrophic respiration relative to the amount of carbon inputs. We summarize and interpret how the saltwater and P legacies differentially influenced ecosystem components and metabolic pathways to understand the recovery trajectory of restored wetlands and its implication for freshwater restoration in the Florida Everglades.

Saltwater and P Legacies on Net Ecosystem Carbon Storage

Although elevated saltwater previously reduced sawgrass growth, sawgrass exposed to elevated saltwater had higher growth during freshwater restoration. Freshwater restoration increased sawgrass aboveground biomass in the legacy saltwater and legacy saltwater and P treatments. These increases in restored sawgrass growth and increased biomass are likely explained by increased nutrient use efficiency (i.e. a molar C:P ratio in sawgrass leaves), which increased 56–70% in the saltwater legacy plots compared to 7% in FW plots. Additionally, belowground biomass increased in the legacy saltwater and legacy saltwater and P treatments during restoration. Although not measured in this study, increased growth in recovering *Cladium jamaicense* plants could have been facilitated by arbuscular mycorrhiza (Jayachandran & Shetty 2003), which can reduce salt stress through nutrient and water acquisition and enhance photosynthetic efficiency (Evelin et al. 2009 and references therein). Our results suggest that freshwater *C. jamaicense* growth and biomass were temporarily inhibited by elevated saltwater but were resilient once the salinity stress was mitigated by freshwater restoration.

Freshwater restoration must take into account how legacies of saltwater and nutrients may affect ER and GEP differently. Some degree of carbon imbalance was expected, especially during early restoration because enhanced plant respiration often comes before recovering photosynthesis under stress (Flexas et al. 2005). However, this imbalance persisted throughout our study, in part because the saltwater legacy increased autotrophic and heterotrophic respiration relative to GEP. The disproportionate saltwater effect on ER might be caused by a reduction in nutrient resorption efficiency for photosynthesis (i.e. a nutrient-conserving mechanism that transfers nutrients from senesced to green leaves, [Aerts 1996]) and an enhancement of respiration from nutrient-enriched litter. This phenomenon was observed in sawgrasses grown in P-enriched soils

(>500 μg g^{-1} P) (Richardson et al. 1999) due to enhanced microbial P assimilation and immobilization into the surface soil or leaf litter (Debusk & Reddy 2005; Pivničková et al. 2010). In our study, average soil P content exceeded the enrichment threshold (543 μg g^{-1} P) only in the SWP legacy treatment. Also, P concentrations were higher in leaf litter than live sawgrass leaves in marshes with previous exposure to elevated saltwater and P.

Previous studies have highlighted the geochemical and biological pathways that can enhance the role of internal P loading in response to P enrichment. There are multiple mechanistic pathways of P legacies in wetlands, including growth-dependent P storage in photosynthetic communities (Newman et al. 1996; Noe et al. 2002; Gaiser 2009), redox-dependent P retention in flocculent sediments (Reddy et al. 1999), redox-dependent microbial uptake (Newman & Reddy 1993), pH-mediated P release (Dierberg et al. 2002), anoxia-promoted P release (Parsons et al. 2017), macrophyte translocation of P from soil to water column (Noe & Childers 2007), and faunal regeneration of P from leaf litter or plankton to higher trophic levels (Schindler et al. 1993; Hagerthey et al. 2014). In P-limited ecosystems like the Everglades, P legacies can affect the storage and cycling of P even after nutrient inputs are reduced or removed (Childers et al. 2019; Sarker et al. 2020). Therefore, nutrient legacies might persist longer than saltwater legacies, and the differential reduction in the multiple disturbance legacies complicates predictions for recovery of carbon balance in coastal ecosystems (Tully et al. 2019).

Freshwater Restoration and Net Ecosystem Carbon Storage

Our measurements of net autotrophic conditions (net carbon sink) in control wetlands were within the high end of reported NEP values (−32–91 g C m^{-2} $year^{-1}$) from a short-hydroperiod, freshwater sawgrass marsh (Zhao et al. 2019). In contrast, net heterotrophic conditions (net carbon source) measured from legacy treatment wetlands were an order of magnitude lower than the lowest reported in situ rates of NEP from the same short-hydroperiod, freshwater sawgrass marsh (Zhao et al. 2019). Our results suggest that legacy effects of saltwater and P in Everglades marshes might cause degraded wetlands to be persistent as net carbon sources.

Elevation loss from saltwater intrusion appears to be a reinforcing positive feedback on reducing net ecosystem productivity and net ecosystem carbon storage. Our findings of net ecosystem heterotrophy in sawgrass wetlands that were previously exposed to elevated saltwater with and without added P, and that subsequently all lost soil elevation, underscore the importance of soil elevation to net ecosystem carbon storage. Assuming constant soil carbon contents and bulk densities, modeled NEP rates were extrapolated to a change in soil elevation in experimental monoliths. For example, average NEP in FW plots (7.6 g C m^{-2} mo^{-1}) was divided by soil carbon content (0.45 g C g-$soil^{-1}$) and bulk density (0.14 g-soil cm^{-3}), resulting in 1.4 mm $year^{-1}$ in the 2018 water year. The rate is within a range of vertical accretion rates (1.6 mm $year^{-1}$) in unenriched portions of central and southern Everglades where sawgrass was the dominant emergent vegetation (Craft & Richardson 1993, 1998). In the legacy plots, net heterotrophic rates translate into a loss of soil elevation at a rate of −6.3 mm $year^{-1}$ in FWP, −7.1 mm $year^{-1}$ in SW and − 12.5 mm $year^{-1}$ in SWP. Assuming a 150 cm ground level, constant elevation changes, and a local sea-level rise (7.7 mm $year^{-1}$ [Dessu et al. 2018]), it will take 60 years to reach a 30-cm soil thickness, below which soil depths cannot support roots' structural integrity. Yet our prediction is likely conservative because other confounding factors, such as gravity compaction and seasonal hydrologic cycle, can accelerate soil organic carbon loss (Cahoon et al. 2011; Day et al. 2011).

The lack of seasonality in carbon fluxes within our mesocosm study was likely caused by constant (approximately 10 cm) water inundation. This stationarity condition differs from the historical Everglades, where water depths fluctuated seasonally from below-ground levels to a high of about 45 cm in sawgrass ridges (McVoy 2011). A comparison of sawgrass biomass across a hydrologic gradient provides insight into the optimal condition for sawgrass growth; an annual average water depth of 10–20 cm results in the highest growth (Childers et al. 2006). Flooding might suppress soil organic carbon mineralization (Neubauer et al. 2000; Wilson et al. 2018) during the dry season when the soil surface is typically re-aerated. Thus, our experimental design might have a marginally positive impact on sawgrass productivity but underestimate microbial respiration on an annual basis.

Nutrient enrichment and saltwater intrusion often lead to plant community shifts in wetlands. Our model prediction did not consider a shift in the macrophyte community from sawgrass to other emergent vegetation (e.g. *Typha domingensis*, *Eleocharis interstincta*) because macrophytes did not change their diversity or composition in response to nutrient enrichment during our mesocosm study, similar to other in situ studies (Craft et al. 1995; Chiang et al. 2000). However, previous studies documented marsh-mangrove transition zones (ecotones) encroaching inland with saltwater in the coastal Everglades (Ross et al. 2000). Increased seawater inundation favors the growth and expansion of mangroves that build up organic compounds belowground fast to keep up with rising sea levels (McKee et al. 2007). For example, in mangrove wetlands, soil accretion rate ranges from 2 to 8 mm $year^{-1}$ (McKee 2011; Krauss et al. 2017). Therefore, future studies should address the potential change of soil accretion rate associated with a vegetation community transition (e.g. Breithaupt et al. 2020).

Freshwater restoration can reduce the rates of saltwater intrusion, while also supporting the recovery of carbon balance in wetlands with previous exposure to saltwater. The capacity of ecosystems to retain stored carbon is enhanced where slow biogeochemical processes predominate (Newman et al. 2017; Ratajczak et al. 2017). However, rapid carbon losses with disturbance are difficult to regain in oligotrophic ecosystems (Kominoski et al. 2018; Gaiser et al. 2020). The remnant ecosystems of the Florida Everglades are highly hydrologically modified and engineered, yet they are undergoing rapid freshwater restoration (Childers et al. 2019; Sarker et al. 2020). Reestablishing freshwater discharge and restoring historical flow pattern are critical to mitigate saltwater intrusion (Kaplan et al. 2010) and are a fundamental goal of Everglades restoration (NASEM 2018). Although we found little evidence of short-term (16 months) recovery of carbon balance in marshes with collapsed soils, freshwater restoration efforts in coastal ecosystems is critical for preventing stored carbon loss in more intact ecosystems. Our study found that saltwater and P legacies transformed freshwater peat wetlands into net carbon sources, despite more than a year of freshwater restoration, suggesting slow recovery of net ecosystem carbon storage in nutrient-limited freshwater wetlands exposed to saltwater intrusion. Our modeled results of reduced NEP in wetland mesocosms at low concentrations of porewater salinity (approximately 2 ppt) from legacy saltwater treatments are similar to field measurements made at similar porewater salinities including: field-based salinity dosing studies in freshwater marshes of the Everglades (Wilson et al. 2018), freshwater tidal marshes of the Altamaha River (Herbert et al. 2018), and tidal brackish marshes in the Mobile Bay (Wilson et al. 2015) and Delaware River estuaries (Weston et al. 2011). Sustained freshwater restoration must reverse legacies of saltwater intrusion and nutrient enrichment to increase net ecosystem carbon storage that is necessary to protect coastal ecosystems exposed to sea-level rise.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Ecosystem metabolism

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