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Causal mechanisms of soil organic matter decomposition: deconstructing salinity and flooding impacts in coastal wetlands

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Abstract. Coastal wetlands significantly contribute to global carbon storage potential. Sea-level rise and other climate-change-induced disturbances threaten coastal wetland sustainability and carbon storage capacity. It is critical that we understand the mechanisms controlling wetland carbon loss so that we can predict and manage these resources in anticipation of climate change. However, our current understanding of the mechanisms that control soil organic matter decomposition, in particular the impacts of elevated salinity, are limited, and literature reports are contradictory. In an attempt to improve our understanding of these complex processes, we measured root and rhizome decomposition and developed a causal model to identify and quantify the mechanisms that influence soil organic matter decomposition in coastal wetlands that are impacted by sea-level rise. We identified three causal pathways: (1) a direct pathway representing the effects of flooding on soil moisture, (2) a direct pathway representing the effects of salinity on decomposer microbial communities and soil biogeochemistry, and (3) an indirect pathway representing the effects of salinity on litter quality through changes in plant community composition over time. We used this model to test the effects of alternate scenarios on the response of tidal freshwater forested wetlands and oligohaline marshes to short- and long-term climate-induced disturbances of flooding and salinity. In tidal freshwater forested wetlands, the model predicted less decomposition in response to drought, hurricane salinity pulsing, and long-term sea-level rise. In contrast, in the oligohaline marsh, the model predicted no change in response to drought and sea-level rise, and increased decomposition following a hurricane salinity pulse. Our results show that it is critical to consider the temporal scale of disturbance and the magnitude of exposure when assessing the effects of salinity intrusion on carbon mineralization in coastal wetlands. Here, we identify three causal mechanisms that can reconcile disparities between long-term and short-term salinity impacts on organic matter decomposition.

Key words: carbon; causal model; decomposition; drought; flooding; hurricane; oligohaline marsh; salinity; sea-level rise; soil organic matter; structural equation model; tidal freshwater forested wetlands.

Introduction

Given that rising temperatures and sea levels are a "virtual certainty" in the next century (IPCC 2013), it is critical that we understand the underlying causal mechanisms to predict and manage for these changes. Predicting ecosystem responses to climatic drivers is important not only for habitat conservation and restoration, but also for understanding how habitat transitions will reflect changes in ecological functions and services such as carbon cycling and storage (Hopkinson et al. 2012). Sea-level rise and salt water intrusion in wetlands have the potential to alter soil carbon stocks through changes in nitrogen, phosphorus, and carbon mineralization (Weston et al. 2006, Jun et al. 2013, Noe et al. 2013). These functions are linked through feedback mechanisms to organic matter production and decomposition (Brinson et al. 1981, Chen and Twilley 1999), which ultimately influence the net accumulation of carbon in the soil, and subsequent surface elevation and wetland sustainability (Kirwan and Blum 2011).

Soil organic matter decomposition is the breakdown of plant and animal detritus through leaching and decomposer activity and is a primary mechanism for carbon loss in wetlands (Howes et al. 1985). The rate of

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decomposition is influenced by external environmental parameters such as temperature, oxygen and nutrient availability, and salinity (Guo et al. 2008), and intrinsic parameters such as microbial community composition (Keiluweit et al. 2015) and detritus quality (Morris and Lajtha 1986). It is well-documented that decomposition rates will increase with increasing temperature and oxygen and nutrient availability (Godshalk and Wetzel 1978), and labile carbon will decompose at a faster rate than refractory carbon (Melillo et al. 1982).

However, patterns of carbon loss with increasing salinity are not consistent in the literature (Weston et al. 2006, Chambers et al. 2013, Neubauer 2013), and these differences may be attributed to varying temporal scales of exposure. For example, the plant and microbial community composition in a freshwater wetland experiencing an acute exposure to increased salinity will be substantially different from a freshwater wetland undergoing sea-level rise-induced habitat transition to a more salt-tolerant ecosystem (chronic exposure; Hopfensperger et al. 2014). Thus, the causal mechanisms controlling decomposition at the acute and chronic scale may differ according to the efficiency of the active decomposer community as well as the carbon source (Neubauer et al. 2013). Until we identify both the direction of the response trajectory, and the temporal scale at which these impacts will be resolved, we cannot accurately estimate carbon storage for future sea-level rise scenarios. The same holds true for decomposition processes in all ecosystems; our affinity for univariate statistical procedures can cloud our understanding of true causal mechanisms (Grace et al. 2016).

To better understand the controls on decomposition in wetlands experiencing sea-level rise, we developed a structural equation model (SEM) to test causal mechanisms of organic matter decomposition along a landscape-scale gradient of increasing salinity that incorporated a habitat transition from tidal freshwater forested wetland to oligohaline marsh. We asked the following questions: (1) What causal mechanisms control soil organic matter decomposition along the landscape gradient? (2) How does soil organic matter decomposition in these four habitats change with alternative flood and salinity scenarios occurring over different temporal scales?

We hypothesized that decomposition would vary across a gradient of salinity and flooding by two distinct pathways: (1) a direct pathway representing the effects of salinity and flooding on decomposer microbial communities and soil biogeochemistry and (2) an indirect pathway representing the effects of salinity and flooding on litter quality through changes in plant community composition over time.

METHODS

Study location

We used a space-for-time substitution approach to quantify patterns of decomposition along a landscape-scale salinity gradient from tidal freshwater forested wetland to oligohaline marsh. We selected sites along the coastal reaches of two rivers, the Waccamaw River and the Savannah River, to represent replicate landscape transects as described in Krauss et al. (2009). Both tidal rivers are located in the southeastern United States and flow into the Atlantic Ocean. Tides along both river systems are semi-diurnal. The mean tidal range is 2.3 and 1.1 m for the Savannah River and Waccamaw River, respectively (NOAA; data *available online*).[4]

Each landscape transect started approximately 30 river-km upstream and extended toward the river mouth along a salinity gradient that included four sites: a tidal freshwater forest (upper forest, 0–0.1 ppt), a low-oligohaline tidal forest (middle forest; 0.5–2.1 ppt), a moderate-oligohaline tidal forest (lower forest; 1.7–3.9 ppt), and a high-oligohaline marsh (marsh; 3.3–4.7ppt; S1–S4 for Savannah sites, W1–W4 for Waccamaw River sites; Fig. 1). The upper forest sites were characterized by a diverse overstory community that was dominated by *Taxodium distichum*, *Nyssa aquatica*, and *Nyssa biflora*. As salinity increased downstream, the overstory community declined, and the herbaceous understory became more dominant. Herbaceous species completely dominated the marsh sites, which were composed of *Spartina cynosuroides*, *Schoenoplectus robustus*, *Typha latifolia*, and *Zizaniopsis miliacea* (Ensign et al. 2014).

Environmental parameters

PVC wells were inserted on each site to measure water level and porewater salinity. A screened, 7.6-cm-diameter pipe was inserted to approximately 1 m into the soil and used to measure in-wetland water level on each site using a pressure sonde (model no. 138; Infinities USA, Port Orange, Florida, USA). Water level was recorded hourly starting in 2005. Mean flood depth was calculated as the water depth above the soil surface during flood events, which were defined as periods where water elevation was greater than wetland surface elevation, averaged over the study period. Four additional, screened 3.8 cm diameter PVC pipes were inserted at the corners of established forest structural plots on each site to a depth of 60 cm, and porewater salinity was measured monthly using a portable conductivity meter (YSI Model 30; YSI, Yellow Springs, Ohio, USA) after wells were pumped of residual water and allowed to refill. Mean salinity was calculated as the average of monthly porewater samples over the study period (October 2010–October 2011).

Reduction–oxidation (redox) potential was measured using platinum electrodes (Faulkner et al. 1989) during root litterbag installation (October 2010) and final root litterbag retrieval (October 2011). Three replicate redox probes were installed to each of three depths (5, 10, and

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[4] http://tidesandcurrents.noaa.gov/sltrends/sltrends_station.shtml?stnid=8665530

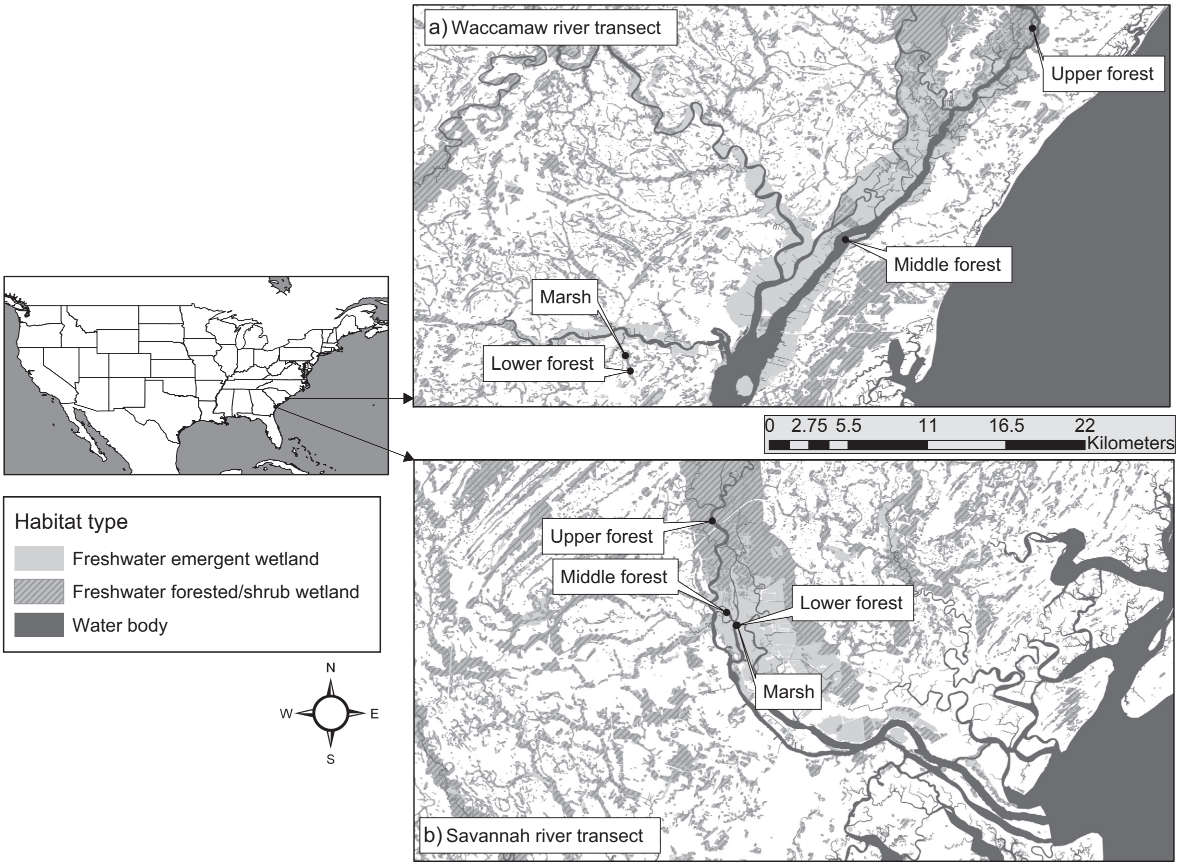

FIG. 1. Study location of the upper forest, middle forest, lower forest and oligohaline marsh, respectively, on the (a) Waccamaw River (W1–W4) and (b) Savannah River (S1–S4) landscape transects.

50 cm) near each of the root litterbag plots in each site (total 180 probes per event). Redox probes were allowed to equilibrate in the soil for at least 30 min before millivolt readings were recorded. One soil temperature sensor was installed at each site to a depth of 10 cm below the soil surface, and hourly temperature measurements were recorded continuously over the study period.

Soil organic matter decomposition

We used the litterbag technique (Hackney and de la Cruz 1980) to measure belowground decomposition of roots and rhizomes (hereafter, "root litterbags"), which integrates several phases of decomposition and represents long-term soil processes. Two root litterbag plots were established at each of the sites along the landscape transects, with the exception of the upper forest sites (four plots per upper forested site), where root litterbag plots were replicated in hummocks and hollows to capture the significant variation in microtopography (Duberstein et al. 2013). Live roots and rhizomes were collected from each site, rinsed and allowed to air-dry, and a known mass (5 g) was placed in the litterbags. Within each plot, six root litterbags (0.8-mm mesh), containing roots and rhizomes collected from the respective site, were inserted into the soil to each of three depths (10, 25, and 50 cm). After installation, single bags were retrieved from each depth at six intervals following a model of hypothesized exponential decay (0.5, 1, 3, 6, 9, 12 months after installation). After retrieval, the root litterbags were gently rinsed with deionized water over a 1-mm sieve, and the remaining biomass was oven-dried to a constant mass at 60°C. We estimated oven-dry mass for the initial air-dried biomass using conversion factors calculated from subsamples for each site. Additionally, three subsamples of the initial root and rhizome material from each site were analyzed for lignin content using the acid-detergent fiber and acid-insoluble ash techniques (Van Soest and Wine 1968).

Model development

Data preparation.—This sampling scheme resulted in a total of 360 root litterbags, which generated six time series of biomass remaining for each middle forest, lower forest, and marsh site and 12 time series of biomass remaining for each upper forest site for a total of 60 time series. The proportion of biomass remaining was calculated for each root litterbag by dividing the oven-dry mass of the remaining biomass by the oven-dry mass of the initial biomass. Missing values were interpolated by using the average of the values observed before and after the missing data point. Of the 360 biomass remaining estimates, 20 (5.6%) were missing. In some cases, surrounding roots grew into the root litterbags and increased biomass from one time to another (Hackney and de la Cruz 1980, Blum 1993, Middleton and McKee 2001). Since decomposition can only reasonably decrease litter biomass (or cause no change) over time, we adjusted the data by setting any increasing value equal to the mass observed at the previous time step. This is a conservative correction for the effect of root in-growth, because we assume no loss due to decomposition in the absence of root in-growth.

Fitting decomposition time-series.—For each of the 60 time series, decomposition was modeled as an exponential decay described by,

$$B_{ij}(t) = a_{ij} + (1 - a_{ij})e^{-b_j t} + \varepsilon_{ij,t}$$

where $B_{ij}(t)$ is the percentage of biomass remaining of litter sample i, in plot j at time t. The parameters a_{ij} and b_j are the asymptote (non-decomposable fraction remaining) and exponential rate constant, respectively (Weider and Lang 1982). To account for potential non-independence caused by the structure of the data collection process, in which plots were grouped in sites, the exponential decay model was fit using a multi-level modeling approach (Gelman and Hill 2007). Based on visual inspection of the data (i.e., the large variation among plots within sites) we chose to allow asymptote parameters a_{ij} to vary at the level of the litter sample (plot-level) and rate parameters b_j to vary at the level of site to account for site-level correlation in uncertainty of plot-level coefficients. This approach gave us the most flexibility to fit the obvious variation in the asymptote (a_{ij}) among plots, while constraining fits based on site-level variation to give us interpretable values for each parameter. Bayesian estimation using Markov chain Monte Carlo (MCMC) simulation implemented in JAGS (Plummer 2014) was used to estimate model parameters. The error, $\varepsilon_{ij,t}$, was modeled with a Gaussian distribution with non-informative Inverse Gamma distributed priors. The priors on a and b were selected to be non-informative Beta and Gaussian distributed, respectively. Plotting the exponential decay models against the observed data illustrates a good fit, indicating appropriate model selection (Fig. 2; Appendix S1: Table S1).

Structural equation model.—We used the mean values of the estimated posterior distributions for the non-decomposable fraction remaining (asymptote, a_{ij}; $n = 60$) and exponential decomposition rate constant (b_j; $n = 8$) as variables for a causal network analysis using a graph theory approach to fitting structural equations models (SEM; Grace et al. 2012). The causal network of the system (Fig. 3) represents a causal hypothesis. We use Pearl's (2000) functional definition of causation, which states that an intervention in the variable at the tail of the arrow would change the observed value in the variable at the tip of the arrow if all other variables were held constant. As such, the direction of each arrow, which represents a hypothesized causal effect, must generally be defended with evidence other than statistical fit, since many different casual networks may have identical statistical fits.

We hypothesized that observed rates of decomposition would vary across an environmental gradient of salinity and flooding due to two distinct pathways: (1) a direct pathway mediated, presumably, by the effects of salinity and flooding on decomposer communities and (2) an indirect pathway mediated through the effect of salinity and flooding on soil biogeochemistry and plant community composition (Fig. 3a). For an example of how SEMs allow for the calculation of direct and indirect effects see Appendix S2. To test the hypotheses and estimate the effects described, we selected specific measures to stand in for each of the concepts (Fig. 3b). We chose mean salinity (ppt) and mean flood depth (cm) as measures of salinity and flooding. We chose biomass production of herbaceous plants ($\mathrm{g \cdot m^{-2} \cdot yr^{-1}}$) to estimate plant community composition, soil reduction–oxidation potential (mV) as a measure of soil oxygen availability, and the relative lignin content of initial litter biomass as a measure of litter quality. Finally, we used both estimated values of the non-decomposable fraction remaining (asymptote, a_{ij}) and the exponential decay rate constant (b_j) as measures of decomposition.

Because we wished to use the results of the model for predictive purposes, we chose transformations, functional and distributional assumptions that would keep predicted values in logical ranges. Additionally, because non-linear responses are common in tidal wetlands (Marani et al. 2010, Osland et al. 2014), we explored both linear and non-linear relationships in selection of the best-fit models (Table 1; Appendix S1: Table S1).

Data structure.—The data for the variables in the causal diagram (Fig. 3b) were collected at two spatial scales: site and plot. Non-decomposable fraction remaining was estimated at the plot scale ($n = 60$). Flood depth, salinity, herbaceous production, lignin content, redox potential, and exponential rate constant were estimated at the site scale ($n = 8$). Previous work from these sites illustrated that as salinity increased along the gradient, tree production (leaf litterfall) declined, and herbaceous production increased, representing the change from tree- to herbaceous-dominated systems (Ensign et al. 2014). We selected herbaceous production to represent community composition, because data for this variable was available at all sites, whereas leaf litter was only available in the forested sites.

The site-scale salinity variable was comprised of four measurements per site, herbaceous production had 10 measurements per site, redox potential data had 36

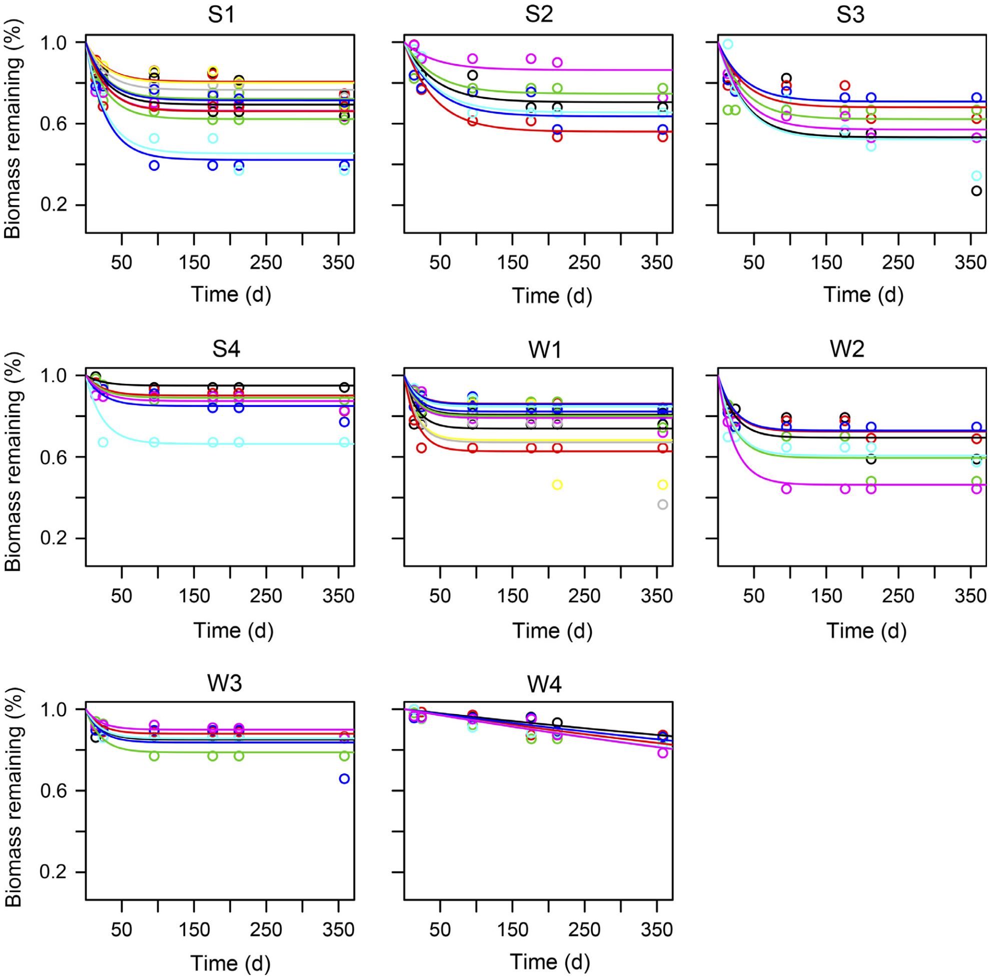

FIG. 2. Time-series of litter decomposition for the upper forest, middle forest, lower forest, and oligohaline marsh, respectively, on the Savannah River (S1–S4) and Waccamaw River (W1–W4) landscape transects. Different line colors represent exponential decay fits for each litterbag plot (n = 6, except sites S1 and W1, n = 12). [Color figure can be viewed at wileyonlinelibrary.com]

measurements per site in the upper forested sites and 18 measurements per site in the other sites, and exponential rate constant had six estimates per site. To account for the different number of observations across variables, SEM fit was assessed using D-sep tests (Shipley 2000). For each pair of variables not connected by an arrow, a determination was made as to which would be causal, or if they should be treated as having correlated errors. The statistical model for each node was updated accordingly and the resulting P value for the added variable was recorded. The information provided by the P values incorporates both the strength of the relationship (relative to noise) and the degrees of freedom of the model. The set of P values for the missing relationships were combined into a single goodness-of-fit test of SEM structure using Fisher's C test (Shipley 2000).

Alternative scenario predictions.—We developed alternate scenarios using empirical data from long-term ecological research conducted on these sites and used the SEM to illustrate how decomposition may respond to potential changes in flooding and salinity associated with short-term disturbance events, such as drought and hurricane storm surge, and long-term sea-level rise (Table 2). Additionally, manipulating one driver while holding the other constant allowed us to assess the relative effects of salinity and flooding on decomposition (Appendix S1: Table S2). In some cases, the empirical data used to develop the scenarios extended beyond the range of data used to parameterize the relationships in the SEM. For the purposes of the alternative scenario predictions, we maintained the functional relationships in the SEM for all scenarios, and the assumptions of these functional and distributional relationships have been clearly described. As is always the case, the robustness of predictions is conditional on the degree to which those assumptions are not violated. Thus, we avoid making additional assumptions that would propose a major shift in the functional relationships outside the range of observed data.

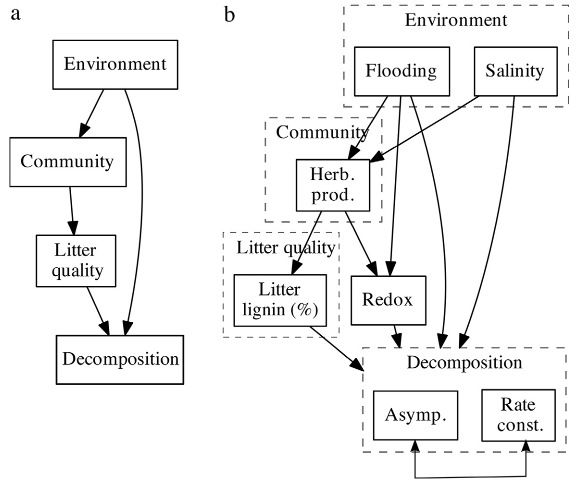

FIG. 3. (a) General and (b) parameterized causal diagrams showing hypothesized direct and indirect effects of salinity and flooding on decomposition of roots and rhizomes. Herb. prod., biomass production of herbaceous plants; assymp., estimated values of the non-decomposable fraction remaining (asymptote); rate const., exponential decay rate constant.

The drought scenario was represented by a decrease in flooding and an increase in salinity. Long-term data collection at these sites provided site-specific flood and porewater salinity data collected during an actual drought event that occurred in 2007–2008 (Cormier et al. 2013). In the drought scenario, mean flood depth and porewater salinity were adjusted by applying the change in flood depth and salinity values between a normal hydrologic year (2010) and a drought year (Waccamaw, 2007; Savannah, 2008). Because the drought scenario was considered a short-term event, decomposition was estimated using the direct pathway of the SEM (Table 2).

To reflect residual storm surge impacts, the hurricane scenario incorporated an increase in salinity, but no change in average flood depth, since flood depth changes from storm surge are temporary in these systems, but elevated salinity porewater salinity can linger (Conner et al. 2007). Porewater salinity data were collected using the same methods as described above as part of a long-term monitoring effort in Louisiana tidal freshwater forested wetlands that coincided with Hurricane Rita in 2005 (Conner et al. 2007). We applied acute fluctuations in mean annual porewater salinity values observed in Louisiana following Hurricane Rita to site-specific mean annual porewater salinity values to simulate salinity changes that might occur from a similar surge along the Savannah and Waccamaw River landscape transects to predict decomposition through the direct pathway of the SEM.

Long-term sea-level rise (SLR) scenarios were represented by increases in flood depth and salinity. To estimate flood depth associated with long-term SLR, we used regional tide gage data (NOAA, see footnote 4) and site-specific wetland surface elevation change data (Stagg et al. 2016) to calculate wetland relative sea-level rise ($\mathrm{RSLR_{wet}}$, Cahoon 2015), which is the difference between relative SLR (long-term) measured at the tide gage and local wetland soil surface elevation change. To estimate increases in salinity, we used local porewater salinity data collected over the period of study (October 2011–October 2012) and projected increases to reflect a shift to the next habitat along the landscape gradient previously described. Decomposition was estimated using both the direct and indirect pathways of the SEM (Table 2).

All statistical analyses, model development, and alternate scenarios testing were conducted in R (R Core Team 2013).

RESULTS

Causal mechanisms

The relationships hypothesized in the causal diagram (Fig. 3a, b) differed from the relationships in the final SEM (Fig. 4). A number of the paths proposed in the hypothetical causal model lacked statistical support from this data set. Specifically, we found no support for an effect of (1) flood depth on herbaceous productivity, (2) herbaceous productivity on redox potential, (3) redox potential on either of the decomposition metrics (asymptote and exponential rate constant), (4) flood depth on the exponential rate constant, or (5) lignin content on

TABLE 1. Distributions, link functions, and parameter values for final structural equation model (SEM).

Variable	Distribution	$F(y\|X)$	β_0	β_1	β_2	β_3	β_4
Herbaceous production, h	gamma	$\log(\mu) = \beta_0 + \beta_1 s$	4.94*	0.57*			
Litter lignin, l (%)	Gaussian	$\mathrm{logit}(\mu) = \beta_0 + \beta_1 h$	−0.38*	-7.8×10^{-4}*			
Redox potential, r	Gaussian	$\mu = \beta_0 + \beta_1 f$	−191.42*	−6.13*			
Asymptote, a	Gaussian	$\mathrm{logit}(\mu) = \beta_0 + \beta_1 s + \beta_2 s^2 + \beta_3 f + \beta_4 l$	−0.317*	0.983*	−0.155*	−0.148*	0.053*
Rate constant, b	Gaussian	$\log(\mu) = \beta_0 + \beta_1 s^2$	−2.79*	−0.14*			

Note: s, salinity; f, flood depth.
$^*P < 0.05$.

Table 2. Flood and salinity data used to model alternate scenarios for drought and hurricane events and long-term sea-level rise (SLR) for different events and SEM causal pathways.

	Flood parameters			Salinity parameters		
Site	Initial flood depth (cm)	Flood change (cm)†	Projected flood depth (cm)	Initial salinity (ppt)	Salinity change (ppt)‡	Projected salinity (ppt)
Short-term drought (2 yr), direct pathway						
S1	4.1	−0.8	3.3	0.1	0.0	0.1
S2	8	−0.1	7.9	1.8	0.4	2.2
S3	6.7	−0.6	6.1	3.4	1.6	5.0
S4	7.2	−0.2	7.0	3.7	1.9	5.6
W1	4.4	−0.3	4.1	0.1	0.0	0.1
W2	12.4	−0.5	11.9	1.2	1.3	2.5
W3	14.9	−0.3	14.6	2.3	1.5	3.8
W4	19.3	−0.9	18.4	4.5	2.1	6.6
Hurricane storm surge (1 yr), direct pathway						
S1	4.1	0	4.1	0.1	0.2	0.3
S2	8	0	8	1.8	2.9	4.7
S3	6.7	0	6.7	3.4	5.4	8.8
S4	7.2	0	7.2	3.7	5.9	9.6
W1	4.4	0	4.4	0.1	0.2	0.3
W2	12.4	0	12.4	1.2	1.9	3.0
W3	14.9	0	14.9	2.3	3.6	5.9
W4	19.3	0	19.3	4.5	7.2	11.7
Long-term sea-level rise (20 yr), indirect and direct pathways						
S1	4.1	1.3	5.4	0.1	1.7	1.8
S2	8.0	0.5	8.5	1.8	1.6	3.4
S3	6.7	−40.8	−34.1	3.4	1.9	5.3
S4	7.2	−26.5	−19.3	3.7	1.9	5.6
W1	4.4	−2.8	1.6	0.1	1.1	1.2
W2	12.4	−2.4	10.0	1.2	1.1	2.3
W3	14.9	12.3	27.3	2.3	2.2	4.5
W4	19.3	−6.8	12.5	4.5	2.2	6.7

Notes: Initial flood depth is the average flood depth relative to the wetland surface over the study period (October 2011–October 2012). Projected flood depth is the sum of the initial flood depth and flood change values. Initial salinity is the average porewater salinity over the study period (October 2011–October 2012). Projected salinity is the sum of the initial salinity and the salinity change values.

† In the drought scenario, flood change is the difference in average annual flood depth between a normal hydrologic year (2009) and a drought year (2007; Cormier et al. 2013). For the hurricane scenario, flood change is assumed to be zero (Conner et al. 2007). In the long-term SLR scenario, flood change is the difference between projected relative SLR and projected wetland elevation ($RSLR_{wet}$). Projected relative SLR = regional relative SLR rate × 20 yr, assuming a constant relative SLR rate of 0.31 cm/y (NOAA gage 8665530; Charleston, South Carolina; http://tidesandcurrents.noaa.gov/sltrends/sltrends_station.shtml?stnid=8665530). Projected wetland elevation = wetland surface elevation change rate × 20 yr. Wetland surface elevation change rates are from Stagg et al. (2016).

‡ In the drought scenario, salinity change is the difference in average annual porewater salinity between a normal hydrologic year (2009) and a drought year (2007; Cormier et al. 2013). In the hurricane scenario, salinity change is the percent change in average annual porewater salinity values observed in Louisiana for the year preceding and following Hurricane Rita for similar sites in Louisiana (Conner et al. 2007). In the long-term SLR scenario, salinity change is the difference between the current average salinity for a given site and the current average salinity for the adjacent higher-salinity habitat. The lower marsh salinity change was also applied to the marsh.

the exponential rate constant. We removed these paths resulting in a better fit between the model and the data ($\chi^2 = 11.45$, df = 11, $P = 0.406$; Fig. 4, Table 1), where the null hypothesis was that the data are derived from the model. The model explained 79% of the variation in herbaceous production, 44% of redox potential variance, 74% of the variance in lignin content, 41% of the variability in the non-decomposable fraction remaining (asymptote), and 39% of the variance associated with the rate of decomposition of root and rhizome material (rate constant).

Supporting our hypotheses, there was a direct effect of salinity on decomposition that was quadratic in nature (Table 1, Figs. 4, 5). The parameter estimates for this relationship (Fig. 4) and the predictive equation (Table 1) represented in Fig. 5 illustrate that decomposition initially declines then increases with increasing salinity. Additionally, we observed that the

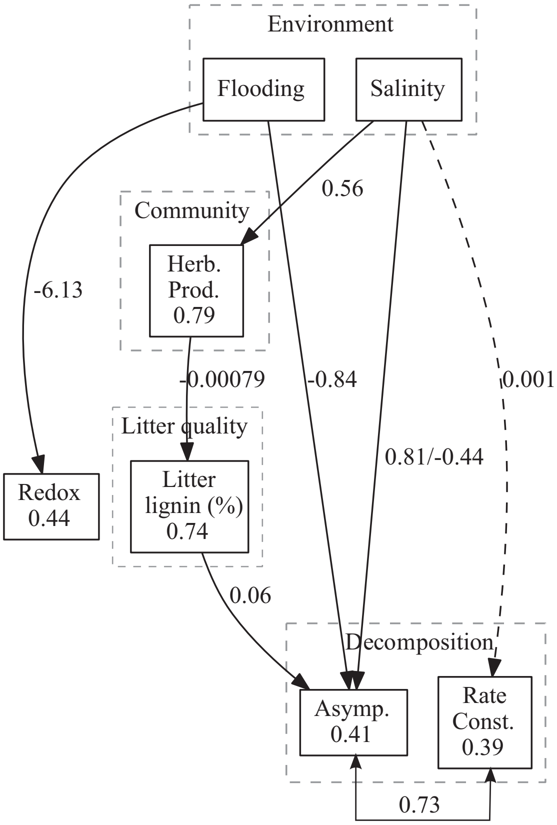

FIG. 4. Structural equation model developed to test direct and indirect effects of salinity and flooding on decomposition of roots and rhizomes. Numbers in boxes are R^2 values that represent variance in decomposition explained by the boxed variable. Numbers associated with arrows are regression coefficients that illustrate the magnitude and direction of the relationships between the variables. The regression coefficient for the direct effect of salinity on the non-decomposable fraction remaining (asymptote) is comprised of a positive and a negative value, which represents the quadratic nature of the relationship.

indirect effects of salinity were modified through community composition and litter quality. Increases in salinity altered community composition from a tree-dominated to an herbaceous-dominated system containing more labile organic matter, or less lignin. Subsequent decreases in lignin content resulted in greater decomposition (Table 1, Figs. 4, 5). The total effect of salinity, combining both direct and indirect causal pathways, was a quadratic response where decomposition was highest in the extreme low and high ends of the salinity gradient, and lowest in the intermediate salinity range (Fig. 5).

Flood depth had a direct negative linear effect on the asymptote, or non-decomposable fraction remaining (i.e., increased flood depth resulted in greater decomposition; Table 1, Fig. 4); however, indirect effects of flood depth on decomposition were not significant. Specifically, the effect of flood depth on decomposition, modified by redox potential, was not significant (Fig. 4). The direct effects of salinity and flooding identified in the SEM were further supported by simultaneous measurements of standard cellulose material (cotton strip technique; Maltby 1988). Regression of cellulose decay rates (CTSL/d) along the landscape gradient showed significant effects of salinity and flooding, which are analogous to direct effects of salinity and flooding presented in the SEM (Appendix S1: Table S3).

Alternative scenario predictions

In response to the drought scenario, the SEM predicted a decline in decomposition in the forested wetland sites and no change in the marsh sites along both the Savannah and Waccamaw River landscape transects (Fig. 6a, d), with the exception of the Waccamaw lower forest. In contrast to all other forested sites, decomposition was predicted to increase in response to drought in the Waccamaw River lower forest (Fig. 6d).

Sites along both rivers showed similar responses to hurricane storm surge (Fig. 6b, e). Relative to the initial conditions, the SEM predicted either minimal change or a slight decline in decomposition in the fresher sites, the upper and middle forests. In the saline sites, the lower forest and marsh, the SEM predicted greater decomposition on both the Savannah and Waccamaw Rivers.

In response to long-term SLR, the SEM predicted a decrease in decomposition in the forested wetland sites

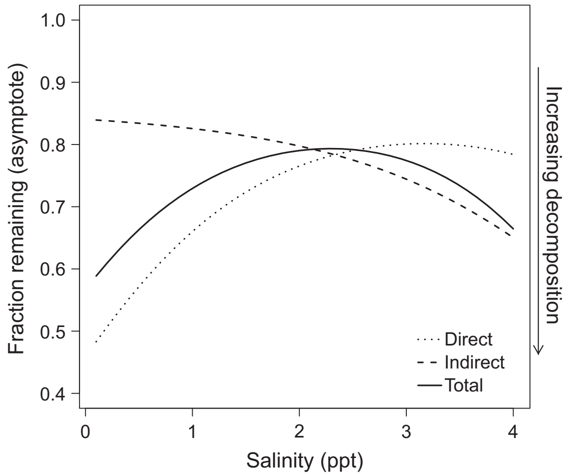

FIG. 5. Predicted response trajectories of organic matter decomposition to increasing salinity for direct (dotted line), indirect (dashed line), and total direct and indirect (solid line) causal pathways.

and no change in the marsh sites along both the Savannah and Waccamaw River landscape transects (Fig. 6c, f), with the exception of the Waccamaw lower forest. In contrast to all other forested sites, decomposition was predicted to increase in response to long-term SLR in the Waccamaw River lower forest (Fig. 6f).

DISCUSSION

Because the fate of wetland soil organic matter is important to multiple ecological feedbacks that ultimately influence wetland sustainability (Kirwan and Blum 2011) and carbon storage (Neubauer 2008), there is significant concern over the potential effect of sea-level rise, in particular increased salinity, on soil organic matter losses (DeLaune and White 2011). However, literature reports examining the response of soil organic matter to increasing salinity are contradictory. For example, recent studies have shown greater decomposition, observed as increasing soil respiration, loss of soil organic carbon, and root decomposition, in soils that

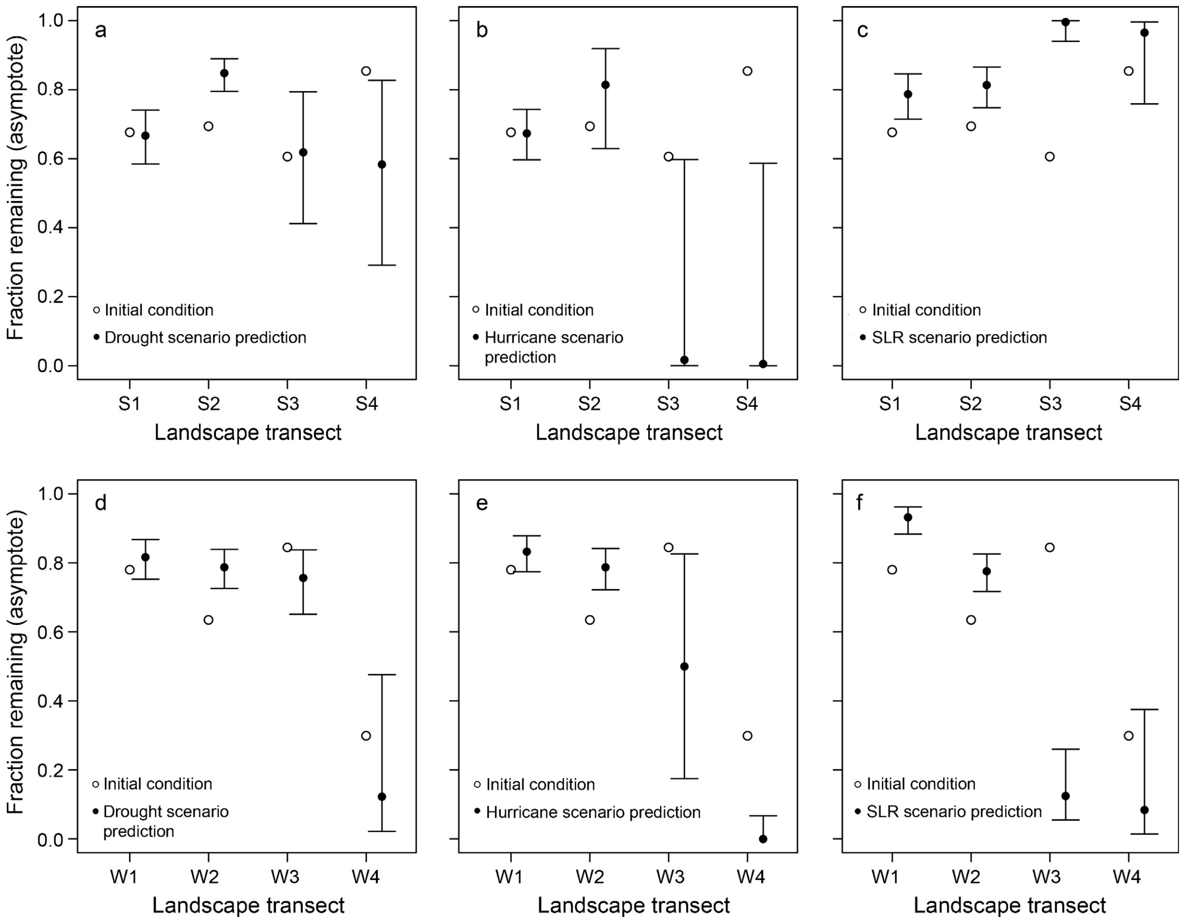

FIG. 6. Scenario projections of decomposition in response to drought (left panel) along the (a) Savannah River and (d) Waccamaw River, hurricane storm surge (middle panel) along the (b) Savannah River and (e) Waccamaw River, and long-term sea-level rise (SLR; right panel) along the (c) Savannah River and (f) Waccamaw River. Error bars represent 95% confidence intervals. As the fraction of material remaining (asymptote) declines, decomposition increases.

were exposed to elevated salinity (Nietch 2000, Weston et al. 2006, 2011, Craft 2007, Chambers et al. 2011), whereas other workers have observed declines in CO_2 emission associated with increasing salinity (Neubauer et al. 2005, Baldwin et al. 2006, Neubauer 2013), a relationship that is also sometimes confounded by hydrology as greater salinity and flooding often coincide (Krauss and Whitbeck 2012, Krauss et al. 2012).

These discrepancies can be attributed to differences in the magnitude and temporal scale of the salinity exposure as described in the conceptual model proposed by Neubauer et al. (2013), who suggested that decomposition in freshwater tidal marshes is impacted through direct and indirect pathways associated with acute and chronic salinity exposures, respectively. Our results clearly support this conceptual model, and further refine the causal mechanisms by defining and quantifying direct and indirect causal pathways of individual salinity and flooding effects on decomposition.

Causal mechanisms

The use of graphic causal modeling allowed us to identify both indirect and direct pathways of litter decomposition along a landscape gradient using statistical controls, which are analogous to experimental controls. The results from our model confirm that decomposition varied across a gradient of salinity and flooding by three distinct pathways: (1) a direct pathway representing the effects of flooding on soil moisture, (2) a direct pathway representing the effects of salinity on decomposer microbial communities and soil biogeochemistry, and (3) an indirect pathway representing the effects of salinity on the quality of the litter through changes in plant community composition over time. Increased flood depth caused greater decomposition, which, through the direct pathway, illustrates the well-documented stimulative effect of moisture on decomposition (Hunt 1978, Howard and Howard 1979, Boddy 1983). Halupa and Howes (1995) found that tidally mediated litter moisture was the primary driver of aboveground litter decay in salt marshes, where changes in flood frequency and duration were correlated with litter moisture, and thus decomposition rates. Furthermore, leaching of dissolved organic carbon from litter upon flooding is one of three primary phases of decomposition (Valiela et al. 1985) that can account for significant mass loss (France et al. 1997, Davis et al. 2003) and is independent of oxygen availability (Godshalk and Wetzel 1978). Although several studies have reported a similar promoting effect of moisture on decomposition (Kruczynski et al. 1978, Montagna and Ruber 1980, Frasco and Good 1982, Newell et al. 1996), others have found that increased flooding inhibited organic matter decay (McKee and Seneca 1982, White and Trapani 1982), or had no significant effect on decomposition at all (Valiela et al. 1985). These inconsistent results indicate that multiple causal pathways are responsible for controlling decomposition, and emphasize the importance of identifying both direct and indirect effects of flooding.

Although it is well-established that increased flooding can lead to anaerobic conditions (Gambrell and Patrick 1978, Ponnamperuma 1984), and slow the rate of decomposition (Tenney and Waksman 1930, Acharya 1935, Tate 1979, Day and Megonigal 1993), we did not find statistical support for an indirect effect of flooding on decomposition that was mediated through redox potential, or oxygen availability. We did find a significant causal link between flooding and redox potential, where, as expected, increasing flood depth reduced soil oxygen availability (Gambrell et al. 1991). However, the link between redox potential and decomposition was not significant. DeLaune et al. (1981) illustrated that decomposition continued to decline beyond the anaerobic threshold (+350 mV) down to −150 mV. However, in our study, redox potential ranged between −196 and −248 mV over the entire study period (data not shown), indicating that the redox potentials observed along this gradient did not vary sufficiently to influence changes in decomposition. Therefore, we do not conclude that an indirect effect of flooding mediated through redox potential does not exist, rather that it is not significantly important in the habitats along this landscape gradient over the course of study. For example, soil redox potentials were higher during drier years (2006–2007) than current along the Savannah River, averaging +127 mV during the driest periods sampled (Krauss and Whitbeck 2012). This indicates that a more exhaustive data set capturing a greater range of redox potentials from these sites would improve the predictive power of the flood pathway. Similarly, we did not find a significant link between temperature and decomposition, and although temperature has been identified as an important factor controlling decomposition (Davidson and Janssens 2006, Giblin et al. 2010, Kirwan et al. 2014), we did not observe large differences in soil temperature along this landscape gradient (data not shown).

In contrast to flooding, our model identified both direct and indirect causal pathways for salinity that predicted different responses depending on the temporal scale of exposure (sensu Neubauer et al. 2013). The short-term effect of salinity on decomposition was expressed through the direct pathway, which we propose represents impacts of salinity on soil biogeochemistry and microbial function. Acute exposures to elevated salinity in freshwater wetland soils can alter decomposition through changes in physicochemical properties, biogeochemical functions and microbial structure and function. Increasing salinity can alter carbon availability by desorbing previously soil-bound organic compounds (Dou et al. 2005). Introduction of alternate electron acceptors can shift microbial function from methanogenesis to the more energy-efficient FeIII reduction (Lowe et al. 2000, Weston et al. 2006) and sulfate reduction (Bartlett et al. 1987, Capone and Kiene 1988). Additionally, microbe populations can be directly inhibited by ionic stress (Wichern et al. 2006, Chambers et al. 2011).

Through the direct pathway, increasing salinity elicited a quadratic response, where decomposition was greatest on either extreme of the salinity gradient, and lowest in the intermediate salinity range (full range 0–4 ppt). These results illustrate that the direction of the response trajectory varied according to the magnitude of exposure, and other studies along estuarine gradients have illustrated a similar non-linear response to increasing salinity (Smith et al. 1983, Nyman and DeLaune 1991). Recent studies that measured the relative effect of short-term salinity increases on methane and carbon dioxide emission provide support for a quadratic response to increasing salinity that is the net result of differential activity by methanogens and sulfate reducers as influenced by the intensity of ionic stress and the availability of electron acceptors, respectively. We propose that the decline in decomposition in the oligohaline marsh is due to simultaneous ionic inhibition of methanogens and electron acceptor limitation of sulfate-reducing bacteria. In flooded soils, researchers have observed a decline in methanogenesis with elevated salinity (Pattnaik et al. 2000, Mishra et al. 2003, Poffenbarger et al. 2011), with significant effects observed as low as 2–3 ppt (Baldwin et al. 2006, Neubauer et al. 2013). This decline in methanogenesis is in part driven by greater availability of the more thermodynamically efficient electron acceptor, sulfate (Bartlett et al. 1987). However, recent research has illustrated that elevated salinity can also directly inhibit methanogens through ionic stress in wetland soils (Baldwin et al. 2006, Chambers et al. 2011).

Although it is well established that sulfate reduction rapidly increases with increasing salinity (Weston et al. 2006), in fresh and low-salinity wetlands the relative contribution of sulfate reduction to overall carbon dioxide emissions is not significant (Vile et al. 2003, Neubauer et al. 2005), and sulfate reduction can be limited below sulfate concentrations of 3 mmol/L (~3.6 ppt salinity, assuming 35 ppt seawater = 28.93 mmol/L sulfate; Pilson 1998; also see Boudreau and Westrich 1984). It is important to point out, however, that the affinity for sulfate (K_s value) varies widely among sulfate-reducing bacterial (SRB) populations, which can coexist in natural sediments (Roden and Tuttle 1993). Therefore, it is possible, depending on the SRB community present in these systems, that the decline in soil organic matter decomposition at intermediate salinity (2–3 ppt) is the result of a simultaneous inhibition of methanogenesis and limited sulfate reduction. Subsequently, as salinity increases beyond the electron acceptor limitation, sulfate reduction, and carbon mineralization increases (Chambers et al. 2011, Weston et al. 2011). Thus, the quadratic response represents a shift from a methanogen-dominated to a SRB-dominated system that is simultaneously stress and resource limited at intermediate salinities along the gradient from fresh to oligohaline wetland (0–4 ppt).

The indirect pathway provides a causal mechanism for the long-term impacts of increased salinity, which are mediated through shifts in plant community structure and subsequent changes in carbon source or litter quality. These changes occur on an annual to decadal scale (Conner et al. 2007), in contrast to the effects described in the direct pathway, which can be resolved within hours to days (Neubauer et al. 2013). Long-term salinity exposure in coastal wetlands, such as observed with sea-level rise, can cause shifts in vegetation community composition and ecological function. For example, salinity intrusion into tidal freshwater forested wetland systems over decades has caused the transition from a forest-dominated community to an herbaceous-dominated system (Krauss et al. 2009). Indeed, these long-term, sustained, changes in environmental condition and vegetation community composition are associated with significant alterations to ecological function, including primary production (Cormier et al. 2013, Ensign et al. 2014), nitrogen and phosphorus mineralization (Noe et al. 2013), greenhouse gas emission (Krauss and Whitbeck 2012), sedimentation (Noe et al. 2016), and surface elevation change (Stagg et al. 2016).

Accordingly, our model identified a significant link between the change in vegetation community composition and decomposition along this landscape-scale gradient. Furthermore, we identified lignin as an important predictor of decomposition as the vegetation community shifts from a forest- to an herbaceous-dominated system. The degree of lignification in plant tissue is known to vary among wetland plant species (McKee and Seneca 1982, Melillo et al. 1982, Buth 1987), and labile plant material decomposes more rapidly compared to tissue with higher lignin content (Maccubbin and Hodson 1980, Hodson et al. 1982, Aber et al. 1990). Therefore, it follows that lignin content is a primary factor controlling differential rates of decomposition across multiple wetland species (Poi de Neiff et al. 2006), which supports our finding that decomposition increased from forested wetland to marsh as the carbon source changed from woody tissue (high lignin content) to herbaceous tissue (low lignin content).

Significant shifts in vegetation community composition along this gradient occur as mean salinity concentrations reach 2 ppt or greater (see also Hackney et al. 2007). Our direct and indirect pathways intersect at this same salinity concentration, reflecting a combination of short-term microbial and long-term vegetation shifts with consequence to ecosystem function. When direct and indirect salinity effects are combined, we might expect a buffered response in the fresh habitats, where the direct and indirect effects oppose each other, and a synergistic effect in the oligohaline wetlands (3–4 ppt), where the two pathways converge to stimulate decomposition.

Alternative scenario predictions

To demonstrate combined direct and indirect effects of flooding and salinity on decomposition and predict the response of tidal forests to climate change-induced disturbances, we tested three alternate scenarios that incorporated different combinations of flooding and salinity manipulations. We simulated drought, hurricane, and sea-level rise, which are disturbance events that will likely impact these coastal systems with increasing frequency in a future with climate change (IPCC 2013).

The drought scenario response was predicted using the direct or short-term pathway for flooding and salinity. Increasing salinity and decreasing flood depth caused significant declines in decomposition in the forested wetland sites, with the exception of the Waccamaw lower forest, which increased, and no change in the marsh sites. Studies in wet ecosystems with anaerobic soils have shown that short-term drought can stimulate carbon loss through soil aeration (Christensen et al. 1998, Alm et al. 1999) and increase the availability of labile carbon and nutrients upon subsequent rewetting (Reddy and Patrick 1975, Fenner and Freeman 2011), responses that are primarily controlled through changes in redox potential. However, the response of soil respiration to drought is variable depending upon the duration and magnitude of drying (Laiho 2006, Worrall et al. 2006), and studies in forested wetlands have shown that decomposition increases in flooded compared to non-flooded conditions (Brinson et al. 1981, Lockaby et al. 1996). Furthermore, the combined effects of elevated salinity and reduced moisture in previously fresh soils can heighten osmotic stress and limit microbial activity (Yuan et al. 2007). These findings support our conclusion that declining decomposition in the forested wetland sites represents the synergistic negative effects of limited soil moisture and salinity-induced ionic stress on microbial populations. In contrast, sustained decomposition rates in the marsh demonstrate the buffering effect of the opposing forces of limited soil moisture (diminished decomposition) and high salinity (enhanced sulfate reduction), where salinity-tolerant sulfate reducers (Chambers et al. 2011) overcome the negative effects of reduced soil moisture.

It is important to note that if the indirect flood effect, mediated through redox potential, was significant, we might expect an increase in predicted decomposition in response to drought, since drought is known to elevate redox potentials (Krauss and Whitbeck 2012). However, the data set used to develop the SEM did not include observations during prolonged dry periods with increased redox potential, which indicates the need for a more comprehensive data set to capture the full range of soil redox conditions in these sites.

The impacts of a hurricane salinity pulse were predicted using the direct or short-term pathway. In response to short-term salinity increases and a constant flood depth, we observed subtle declines in decomposition in the upper and middle forests, and an increase in decomposition in the lower forests and marshes. Reduced decomposition in the upper and middle forested wetland sites reflects the shift to the intermediate salinity zone, where salinity directly inhibits decomposition. We were not able to find any studies that examined hurricane impacts on soil organic matter decomposition in a freshwater forested wetland to support these predictions. However, recent studies in freshwater marsh soils reported declines in ecosystem soil respiration with elevated salinity, which supports our alternate scenario predictions (Neubauer 2013). In mangroves, Barr et al. (2012) reported significant hurricane impacts to soil CO_2 flux, latent heat flux, and nighttime net ecosystem exchange, which originated from wind damage to the forest canopy. Additionally, mangrove studies identify root decomposition as a primary factor influencing soil surface elevation following hurricane-induced tree mortality (Lugo 1997, Cahoon et al. 2003), indicating that other drivers in addition to salinity should be considered in the hurricane scenario.

Enhanced decomposition in the lower forested wetland sites and the marsh reflect the direct stimulatory effect of elevated salinity on sulfate reduction. Chambers et al. (2013) also observed similar effects from salinity pulses, which resulted in a 112% increase in soil respiration in freshwater marsh soils. Together, these results indicate that hurricanes, through introduction of elevated porewater salinity, can inhibit soil carbon loss in the upper and middle forests, and accelerate soil carbon loss in the lower forest and marsh. Further work is needed to incorporate the effects of rapid tree mortality on soil carbon losses for hurricane scenarios in tidal freshwater forests.

In contrast to the episodic drought and hurricane disturbances, the long-term SLR scenario incorporated both the direct and indirect effects of salinity, and the direct effects of flooding. The net response to these direct and indirect effects was similar to the drought scenario. The model predicted general declines in decomposition in the forested wetland sites, with the exception of the Waccamaw lower forest, and no change in decomposition in the marsh sites. The decline in the upper and middle forests reflects the short-term influence of intermediate salinity levels on decomposition as well as the long-term, or indirect, effect of salinity through changes in vegetation structure and lignin content. For example, the model predicts that after 20 yr of sea-level rise, the upper and middle forests will shift to the intermediate salinity zone where ionic stress limits decomposition. Additionally, the vegetation community will still be dominated by woody vegetation, with higher lignin content and slower rates of decomposition. In contrast, the marsh sites are predicted to sustain existing rates of decomposition after 20 yr of SLR, reflecting little change in vegetation community composition, litter quality, and salinity regime. Although salinity is projected to increase in this scenario, it is still within the brackish marsh category, which has been observed to be less responsive to additional increases in salinity (Chambers et al. 2013) and flooding (Kirwan et al. 2013).

Coastal wetlands significantly contribute to global carbon storage potential because of their ability to accumulate carbon belowground (Donato et al. 2011). High rates of carbon accumulation in coastal wetlands are often attributed to relatively slow rates of organic matter decomposition and high rates of production. Our model predicts that both short- and long-term disturbances will cause declines in decomposition in tidal forests, indicating that potential carbon storage will increase in tidal forests even as they convert to marsh in the future. Although the tidal forest responds similarly to long- and short-term events, the oligohaline marshes show different responses depending on the time scale of the disturbance event. For example, we predict no net change in decomposition in the oligohaline marshes following a drought or after 20 yr of SLR. However, hurricane salinity pulses will stimulate decomposition in the marsh. Therefore, studies attempting to estimate carbon accumulation for future climate change scenarios that do not consider both long- and short-term impacts on decomposition processes will likely inaccurately assess carbon storage potential.

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Literature Cited

Aber, J. D., J. M. Melillo, and C. A. McClaugherty. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Canadian Journal of Botany 68:2201–2208.

Acharya, C. N. 1935. Studies on the anaerobic decomposition of plant materials. III. Comparison of the course of decomposition under anaerobic, aerobic and partially aerobic conditions. Biochemical Journal 29:1116–1120.

Alm, J., L. Schulman, J. Walden, H. Nykanen, P. J. Martikainen, and J. Silvola. 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology 80:161–174.

Baldwin, D. S., G. N. Rees, A. M. Mitchell, G. Watson, and J. Williams. 2006. The short-term effects of salinization on anaerobic nutrient cycling and microbial community structure in sediment from a freshwater wetland. Wetlands 26:455–464.

Barr, J. G., V. Engel, T. J. Smith III, and J. D. Fuentes. 2012. Hurricane disturbance and recovery of energy balance, CO_2 fluxes and canopy structure in a mangrove forest of the Florida Everglades. Agricultural and Forest Meteorology 153:54–66.

Bartlett, K. B., D. S. Bartlett, R. C. Harriss, and D. I. Sebacher. 1987. Methane emissions along a salt-marsh salinity gradient. Biogeochemistry 4:183–202.

Blum, L. K. 1993. Spartina alterniflora root dynamics in a Virginia marsh. Marine Ecology Progress Series 102:169–178.

Boddy, L. 1983. Carbon dioxide release from decomposing wood: effect of water content and temperature. Soil Biology and Biochemistry 15:501–510.

Boudreau, B. P., and J. T. Westrich. 1984. The dependence of bacterial sulfate reduction on sulfate concentration in marine sediments. Geochimica et Cosmochimica Acta 48: 2503–2516.

Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary production, decomposition and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics 12:123–161.

Buth, G. J. C. 1987. Decomposition of roots of three plant communities in a Dutch salt marsh. Aquatic Botany 29: 123–138.

Cahoon, D. R. 2015. Estimating relative sea-level rise and submergence potential at a coastal wetland. Estuaries and Coasts 38:1077–1084.

Cahoon, D. R., P. Hensel, J. Rybczyk, K. McKee, C. E. Proffitt, and B. C. Perez. 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. Journal of Ecology 91:1093–1105.

Capone, D. G., and R. P. Kiene. 1988. Comparison of microbial dynamics in marine and fresh-water sediments: contrasts in anaerobic carbon catabolism. Limnology and Oceanography 33:725–749.

Chambers, L. G., T. Z. Osborne, and K. R. Reddy. 2013. Effect of salinity-altering pulsing events on soil organic carbon loss along an intertidal wetland gradient: a laboratory experiment. Biogeochemistry 115:363–383.

Chambers, L. G., K. R. Reddy, and T. Z. Osborne. 2011. Short-term response of carbon cycling to salinity pulses in a freshwater wetland. Soil Science Society of America Journal 75:2000–2007.

Chen, R., and R. R. Twilley. 1999. A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. Biogeochemistry 44:93–118.

Christensen, T. R., S. Jonasson, A. Michelsen, T. V. Callaghan, and M. Havstrom. 1998. Environmental controls on soil respiration in the Eurasian and Greenlandic Artic. Journal of Geophysical Research 103:29015–29021.

Conner, W., T. Doyle, and K. Krauss. 2007. Ecology of tidal freshwater swamps of the southeastern United States. Springer, Dordrecht, The Netherlands.

Cormier, N., K. W. Krauss, and W. H. Conner. 2013. Periodicity in stem growth and litterfall in tidal freshwater forested wetlands: influence of salinity and drought on nitrogen recycling. Estuaries and Coasts 36:533–546.

Craft, C. B. 2007. Freshwater input structures soil properties, vertical accretion and nutrient accumulation of Georgia and United States (US) tidal marshes. Limnology and Oceanography 52:1220–1230.

Davidson, E. A., and I. A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173.

Davis III, S. E., C. Corronado-Molina, D. L. Childers, and J. W. Day Jr. 2003. Temporally dependent C, N, and P dynamics associated with the decay of *Rhizophora mangle* L. leaf litter in oligotrophic mangrove wetlands of the Southern Everglades. Aquatic Botany 75:199–215.

Day, F. P., and J. P. Megonigal. 1993. The relationship between variable hydroperiod, production allocation, and belowground organic turnover in forested wetlands. Wetlands 13:115–121.

DeLaune, R. D., C. N. Reddy, and W. H. Patrick Jr. 1981. Organic matter decomposition in soil as influenced by pH and redox conditions. Soil Biology and Biochemistry 13:533–534.

DeLaune, R. D., and J. R. White. 2011. Will coastal wetlands continue to sequester carbon in response to an increase in global sea level?: a case study of the rapidly subsiding Mississippi River deltaic plain. Climatic Change 110:297–314.

Donato, D. C., J. B. Kauffman, D. Murdiyarso, S. Kurnianto, M. Stidham, and M. Kanninen. 2011. Mangroves among the most carbon-rich forests in the tropics. Nature Geoscience 4:293–297.

Dou, F., C. L. Ping, L. Guo, and T. Jorgenson. 2005. Estimating the impact of seawater on the production of soil water-extractable organic carbon during coastal erosion. Journal of Environmental Quality 37:2368–2374.

Duberstein, J. A., K. W. Krauss, W. H. Conner, W. C. Bridges, and V. B. Shelburne. 2013. Do hummocks provide a physiological advantage to even the most flood tolerant of tidal freshwater trees? Wetlands 33:399–408.

Ensign, S. H., G. B. Noe, and C. R. Hupp. 2014. Linking channel hydrology with riparian wetland accretion in tidal rivers. Journal of Geophysical Research: Earth Surface 119:28–44.

Faulkner, S. P., W. H. Patrick, and R. P. Gambrell. 1989. Field techniques for measuring wetland soil parameters. Soil Science Society of America Journal 53:883–890.

Fenner, N., and C. Freeman. 2011. Drought-induced carbon loss in peatlands. Nature Geoscience 4:895–900.

France, R., H. Culbert, C. Freeborough, and R. Peters. 1997. Leaching and early mass loss of boreal leaves and wodd in oligotrophic water. Hydrobiologia 345:209–214.

Frasco, B. A., and R. E. Good. 1982. Decomposition dynamics of *Spartina alterniflora* and *Spartina patens* in a New Jersey salt marsh. American Journal of Botany 69:402–406.

Gambrell, R. P., R. D. DeLaune, and W. H. Patrick. 1991. Redox processes in soils following oxygen depletion. Pages 101–117 *in* M. B. Jackson, D. D. Davies, and H. Lambers, editors. Plant life under oxygen deprivation: ecology, physiology, and biochemistry. SPB Academic Publishing BV, The Hague, The Netherlands.

Gambrell, R. P., and W. H. Patrick. 1978. Chemical and microbiological properties of anaerobic soils and sediments. Pages 375–423 *in* D. D. Hook and R. M. M. Crawford, editors. Plant life in anaerobic environments. Ann Arbor Science, Ann Arbor, Michigan, USA.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Page 607. Cambridge University Press, New York, New York, USA.

Giblin, A. E., N. B. Weston, G. T. Banta, J. Tucker, and C. S. Hopkinson. 2010. The effects of salinity on nitrogen losses from an oligohaline estuarine sediment. Estuaries and Coasts 33:1054–1068.

Godshalk, G. L., and R. G. Wetzel. 1978. Decomposition of aquatic angiosperms. III. *Zostera marina* L. and a conceptual model of decomposition. Aquatic Botany 5:329–354.

Grace, J. B., D. R. Schoolmaster Jr., G. R. Guntenspergen, A. M. Little, B. R. Mitchell, K. M. Miller, and E. W. Schweiger. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere 3:1–44.

Grace, J. B., et al. 2016. Integrative modelling reveals mechanisms linking productivity and plant species richness. Nature 529:390–393.

Guo, X., X. Lu, S. Tong, and D. Guohua. 2008. Influence of environment and substrate quality on the decomposition of wetland plant root in the Sanjiang Plain, Northeast China. Journal of Environmental Sciences 20:1445–1452.

Hackney, C. T., G. B. Avery, L. A. Leonard, M. Posey, and T. Alphin. 2007. Biological, chemical, and physical characteristics of tidal freshwater swamp forests of the lower Cape Fear River/Estuary, North Carolina. Pages 183–221 *in* W. H. Conner, T. W. Doyle, and K. W. Krauss, editors. Ecology of tidal freshwater forested wetlands of the southeastern United States. Springer, New York, New York, USA.

Hackney, C. T., and A. A. de la Cruz. 1980. In situ decomposition of roots and rhizomes of two tidal marsh plants. Ecology 61:226–231.

Halupa, P. J., and B. L. Howes. 1995. Effects of tidally mediated litter moisture content on decomposition of *Spartina alterniflora* and *S. patens*. Marine Biology 123:379–391.

Hodson, R. E., A. E. Maccubbin, and R. Benner. 1982. Microbial degradation of natural and pollutionally-derived lignocellulosic detritus in wetland ecosystems. U.S. Department of the Interior OWRT Project Report no. A-082-GA. U.S. Department of the Interior, Washington, D.C., USA.

Hopfensperger, K. N., A. J. Burgin, V. A. Schoepfer, and A. M. Helton. 2014. Impacts of saltwater incursion on plant communities, anaerobic microbial metabolism, and resulting relationships in a restored freshwater wetland. Ecosystems 17:792–807.

Hopkinson, C. S., W. J. Cai, and X. Hu. 2012. Carbon sequestration in wetland dominated coastal systems – a global sink of rapidly diminishing magnitude. Current Opinion in Environmental Sustainability 4:186–194.

Howard, P. J. A., and D. M. Howard. 1979. Relationship of decomposing litter in relation to temperature and moisture. Oikos 33:457–465.

Howes, B. L., J. W. H. Dacey, and J. M. Teal. 1985. Annual carbon mineralization and belowground production of *Spartina alterniflora* in a New England salt marsh. Ecology 66: 595–605.

Hunt, H. W. 1978. A simulation model for decomposition in grasslands. Pages 155–184 *in* G. S. Innis, editor. Grassland simulation model. Ecological studies 26. Springer-Verlag, New York, New York, USA.

IPCC. 2013. Climate change 2013: the physical science basis. Page 1535 *in* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Jun, M., A. E. Altor, and C. B. Craft. 2013. Effects of increased salinity and inundation on inorganic nitrogen exchange and phosphorus sorption by tidal freshwater floodplain forest soils, Georgia (USA). Estuaries and Coasts 36:508–518.

Keiluweit, M., J. J. Bougoure, P. S. Nico, J. Pett-Ridge, P. K. Weber, and M. Kleber. 2015. Mineral protection of soil carbon counteracted by root exudates. Nature Climate Change 5:588–595.

Kirwan, M. L., and L. K. Blum. 2011. Enhanced decomposition offsets enhanced productivity and soil carbon accumulation in coastal wetlands responding to climate change. Biogeosciences 8:987–993.

Kirwan, M. L., J. A. Langley, G. R. Guntenspergen, and J. P. Megonigal. 2013. The impact of sea-level rise on organic matter decay rates in Chesapeake Bay brackish tidal marshes. Biogeosciences 10:1869–1876.

Krauss, K. W., J. A. Duberstein, T. W. Doyle, W. H. Conner, R. H. Day, L. W. Inabinette, and J. L. Whitbeck. 2009. Site condition, structure, and growth of bald cypress along tidal/non-tidal salinity gradients. Wetlands 29:505–519.

Kirwan, M. L., G. R. Guntenspergen, and J. A. Langley. 2014. Temperature sensitivity of organic-matter decay in tidal marshes. Biogeosciences 11:4801–4808.

Krauss, K. W., and J. L. Whitbeck. 2012. Soil greenhouse gas fluxes during wetland forest retreat along the lower Savannah River, Georgia (USA). Wetlands 32:73–81.

Krauss, K. W., J. L. Whitbeck, and R. J. Howard. 2012. On the relative roles of hydrology, salinity, temperature, and root productivity in controlling soil respiration from coastal swamps (freshwater). Plant and Soil 358:265–274.

Kruczynski, W. L., C. B. Subrahmanyam, and S. H. Drake. 1978. Studies on the plant community of a North Florida salt marsh. Bulletin of Marine Science 28:707–715.

Laiho, R.. 2006. Decomposition in peatlands: reconciling seemingly contrasting results on the impacts of lowered water levels. Soil Biology and Biochemistry 38:2011–2024.

Lockaby, B. G., A. L. Murphy, and G. L. Somers. 1996. Hydroperiod influences on nutrient dynamics in decomposing litter of a flood-plain forest. Soil Science Society of America Journal 60:1267–1272.

Lowe, K. L., T. J. Dichristina, A. N. Roychoudhury, and P. Van Cappellen. 2000. Microbiological and geochemical characterization of microbial Fe(III) reduction in salt marsh sediments. Geomicrobiology Journal 17:163–176.

Lugo, A. 1997. The apparent paradox or reestablishing species richness on degraded lands with tree monocultures. Forestry Ecology and Management 99:9–19.

Maccubbin, A. E., and R. E. Hodson. 1980. Mineralization of detrital lignocelluloses by salt marsh sediment microflora. Applied and Environmental Microbiology 40:735–740.

Maltby, E. 1988. Use of cotton strip assay in wetland and upland environments - an international perspective. Pages 140–154 *in* A. F. Harrison, P. M. Latter, and D. W. H. Walton, editors. The Cotton Strip Assay: An Index of Decomposition in Soils. Proceedings Institute of Terrestrial Ecology Symposium, Grange-over-Sands, UK.

Marani, M., A. D'Alpaos, S. Lanzoni, L. Carniello, and A. Rinaldo. 2010. The importance of being coupled: stable states and catastrophic shifts in tidal biomorphodynamics. Journal of Geophysical Research 115:F04004.

McKee, K. L., and E. D. Seneca. 1982. The influence of morphology in determining the decomposition of two salt marsh macrophytes. Estuaries 5:302–309.

Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626.

Middleton, B. A., and K. L. McKee. 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. Journal of Ecology 89:818–828.

Mishra, S. R., P. Pattnaik, N. Sethunathan, and T. K. Adhya. 2003. Anion-mediated salinity affecting methane in a flooded alluvial soil. Geomicrobiology Journal 20:579–586.

Montagna, P. A., and E. Ruber. 1980. Decomposition of *Spartina alterniflora* in different seasons and habitats of a northern Massachusetts salt marsh, and a comparison with other Atlantic regions. Estuaries 3:61–64.

Morris, J. T., and K. Lajtha. 1986. Decomposition and nutrient dynamics of litter from four species of freshwater emergent macrophytes. Hydrobiologia 131:215–223.

Neubauer, S. C. 2008. Contributions of mineral and organic components to tidal freshwater marsh accretion. Estuarine, Coastal and Shelf Science 78:78–88.

Neubauer, S. C. 2013. Carbon sequestration in wetland soils: importance, mechanisms, and future prospects. SWS Research Brief No. 2013-0001. Society of Wetland Scientists. http://www.sws.org/category/sws-research-briefs.html

Neubauer, S. C., R. B. Franklin, and D. J. Berrier. 2013. Saltwater intrusion into tidal freshwater marshes alters the biogeochemical processing of organic carbon. Biogeosciences 10:8171–8183.

Neubauer, S. C., K. Givler, S. K. Valentine, and J. P. Megonigal. 2005. Seasonal patterns and plant-mediated controls of subsurface wetland biogeochemistry. Ecology 86:3334–3344.

Newell, S. Y., T. L. Arsuffi, and L. A. Palm. 1996. Misting and nitrogen fertilization of shoots of a saltmarsh grass: effects upon fungal decay of leaf blades. Oecologia 108:495–502.

Nietch, C. T. 2000. Carbon biogeochemistry in tidal marshes of South Carolina: the effect of salinity and nutrient availability on marsh metabolism in estuaries with contrasting histories of disturbance and river influence. Dissertation, University of South Carolina, Columbia, South Carolina, USA.

Noe, G. B., C. R. Hupp, C. E. Bernhardt, and K. W. Krauss. 2016. Contemporary deposition and long-term accumulation of sediment and nutrients by tidal freshwater forest wetlands impacted by sea level rise. Estuaries and Coasts 39: 1106–1119.

Noe, G. B., K. W. Krauss, B. G. Lockaby, W. H. Conner, and C. R. Hupp. 2013. The effect of increasing salinity and forest mortality on soil nitrogen and phosphorus mineralization in tidal freshwater forested wetlands. Biogeochemistry 114:225–244.

Nyman, J. A., and R. D. DeLaune. 1991. CO_2 emission and soil Eh responses to different hydrological regimes in fresh, brackish and saline marsh soils. Limnology and Oceanography 36:1406–1414.

Osland, M. J., N. Enwright, and C. L. Stagg. 2014. Freshwater availability and coastal wetland foundation species: ecological transitions along a rainfall gradient. Ecology 95:2789–2802.

Pattnaik, P., S. R. Mishra, K. Bharati, S. R. Mohanty, N. Sethunathan, and T. K. Adhya. 2000. Influence of salinity on methanogenesis and associated microflora in tropical rice soils. Microbiological Research 155:215–220.

Pearl, J.. 2000. Causality: models, reasoning, and inference. Cambridge University Press, New York, New York, USA.

Pilson, M. E. 1998. An introduction to the chemistry of the sea. Prentice-Hall, New York, New York, USA.

Plummer, M. 2014. Package rjags. The comprehensive R archive network. http://cran.r-project.org/

Poffenbarger, H. J., B. A. Needelman, and J. P. Megonigal. 2011. Salinity influence on methane emissions from tidal marshes. Wetlands 31:831–842.

Poi de Neiff, A., J. J. Neiff, and L. C. Sylvina. 2006. Leaf litter decomposition in three wetland types of the Parana River flood plain. Wetlands 26:558–566.

Ponnamperuma, F. N. 1984. Effects of flooding on soils. Pages 1–44 *in* T. T. Kozlowski, editor. Flooding and plant growth. Academic Press, Orlando, Florida, USA.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reddy, K. R., and W. H. Patrick Jr. 1975. Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. Soil Biology and Biochemistry 7:87–94.

Roden, E. E., and J. H. Tuttle. 1993. Inorganic sulfur turnover in oligohaline estuarine sediments. Biogeochemistry 22:81–105.

Shipley, B. 2000. Cause and correlation in biology. Cambridge University Press, Cambridge, UK.

Smith, C. J., R. D. DeLaune, and W. H. Patrick Jr. 1983. Carbon dioxide emission and carbon accumulation in coastal wetlands. Estuarine, Coastal and Shelf Science 17:21–29.

Stagg, C. L., K. W. Krauss, D. R. Cahoon, N. Cormier, W. H. Conner, and C. M. Swarzenski. 2016. Processes contributing to resilience of coastal wetlands to sea-level rise. Ecosystems 19:1445–1459.

Stagg, C. L., D. R. Schoolmaster, K. W. Krauss, N. Cormier, and W. H. Conner. 2017. Organic matter decomposition along coastal wetland landscape gradient from tidal freshwater forested wetland to oligohaline marsh in Southeastern U.S.A. (2010–2011): U.S. Geological Survey Data Release. https://doi.org/10.5066/f73t9fcj9fcj.

Tate, R. L. 1979. Effect of flooding on microbial activities in organic soils: carbon metabolism. Soil Science 128:267–272.

Tenney, F. G., and S. A. Waksman. 1930. Composition of natural organic materials and their decomposition in the soil: V. Decomposition of various chemical constituents in plant materials under an-aerobic conditions. Soil Science 30:143–160.

Valiela, I., J. M. Teal, S. D. Allen, R. Van Etten, D. Goehringer, and S. Volkmann. 1985. Decomposition in salt marsh ecosystems: the phases and major factors affecting disappearance of above-ground organic matter. Journal of Experimental Marine Biology and Ecology 89:29–54.

Van Soest, P. J., and R. H. Wine. 1968. Determination of lignin and cellulose in acid-detergent fiber with permanganate. Journal of the Association of Official Analytical Chemists 51:780–785.

Vile, M. A., S. D. Bridgham, and R. K. Wieder. 2003. Response of anaerobic carbon mineralization rates to sulfate amendments in a boreal peatland. Ecological Applications 13:720–734.

Weider, R. K., and G. E. Lang. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63:1636–1642.

Weston, N. B., R. E. Dixon, and S. B. Joyce. 2006. Ramification of increased salinity in tidal freshwater sediments: geochemistry and microbial pathways of organic matter mineralization. Journal of Geophysical Research 111:1–14.

Weston, N. B., M. A. Vile, S. C. Neubauer, and D. J. Velinsky. 2011. Accelerated microbial organic matter mineralization following salt-water intrusion into tidal freshwater marsh soils. Biogeochemistry 102:135–151.

White, D. A., and J. M. Trapani. 1982. Factors influencing disappearance of *Spartina alterniflora* from litterbags. Ecology 63:242–245.

Wichern, J., F. Wichern, and R. G. Joergensen. 2006. Impact of salinity on soil microbial communities and the decomposition of maize in acidic soils. Geoderma 137:100–108.

Worrall, F., T. P. Burt, and J. K. Adamson. 2006. Trends in drought frequency – the fate of DOC export from British peatlands. Climate Change 76:339–359.

Yuan, B. C., Z. Z. Li, H. Liu, M. Gao, and Y. Y. Zhang. 2007. Microbial biomass and activity in salt affected soils under arid conditions. Applied Soil Ecology 35:319–328.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1890/suppinfo

Data Availability

Data is available from Sciencebase.gov: https://doi.org/10.5066/f73t9fcj9fcj