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RESEARCH ARTICLE

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Direct and indirect controls on organic matter decomposition in four coastal wetland communities along a landscape salinity gradient

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Abstract

- 1. Coastal wetlands store more carbon than most ecosystems globally. As sea level rises, changes in flooding and salinity will potentially impact ecological functions, such as organic matter decomposition, that influence carbon storage. However, little is known about the mechanisms that control organic matter loss in coastal wetlands at the landscape scale. As sea level rises, how will the shift from fresh to salt-tolerant plant communities impact organic matter decomposition? Do longterm, plant-mediated, effects of sea-level rise differ from direct effects of elevated salinity and flooding?
- 2. We identified internal and external factors that regulated indirect and direct pathways of sea-level rise impacts, respectively, along a landscape-scale salinity gradient that incorporated changes in wetland type (fresh, oligohaline, mesohaline and polyhaline marshes). We found that indirect and direct impacts of sea-level rise had opposing effects on organic matter decomposition.
- 3. Salinity had an indirect effect on litter decomposition that was mediated through litter quality. Despite significant variation in environmental conditions along the landscape gradient, the best predictors of above- and below-ground litter decomposition were internal drivers, initial litter nitrogen content and initial litter lignin content respectively. Litter decay constants were greatest in the oligohaline marsh and declined with increasing salinity, and the fraction of litter remaining (asymptote) was greatest in the mesohaline marsh. In contrast, direct effects of salinity and flooding were positive. External drivers, salinity and flooding, stimulated cellulytic activity, which was highest in the polyhaline marsh.
- 4. Synthesis. Our results indicate that as sea level rises, initial direct effects of salinity will stimulate decay of labile carbon, but over time as plant communities shift from fresh to polyhaline marsh, litter decay will decline, yielding greater potential for long-term carbon storage. These findings highlight the importance of quantifying carbon loss at multiple temporal scales, not only in coastal wetlands but also in other ecosystems where plant-mediated responses to climate change will have significant impacts on carbon cycling.

KEYWORDS

carbon, cellulose decay, coastal wetlands, landscape, litter decomposition, plant community, plant-climate interactions, sea-level rise

1 | INTRODUCTION

Climate change-induced shifts in vegetation community composition will have important implications for ecological function (Wolters et al., 2000) and ultimately carbon cycling (Jobbagy & Jackson, 2000). In terrestrial ecosystems, shifts in vegetation community composition have been observed in response to elevated atmospheric carbon dioxide (Leadley, Niklaus, Stocker, & Korner, 1999; Owensby, Coyne, Ham, Auen, & Knapp, 1993), elevated air, soil and water temperatures (Alward, Detling, & Milchunas, 1999; Harte & Shaw, 1995), altered precipitation patterns (Sternberg, Brown, Masters, & Clarke, 1999) and their interactions (Kardol et al., 2010). Coastal marshes, situated between terrestrial and marine ecosystems, are exposed not only to these climatic drivers (Osland et al., 2016; Osland, Enwright, & Stagg, 2014) but also to anthropogenic pressures along the landward boundary and rising sea levels along the seaward boundary (Day et al., 2008; Small & Nicholls, 2003).

Sea-level rise can force shifts in wetland vegetation community composition by altering flooding and salinity regimes (Burdick & Mendelssohn, 1987; DeLaune, Patrick, & Pezeshki, 1987; Hester, Mendelssohn, & McKee, 2001; Krauss et al., 2009; McKee & Mendelssohn, 1989). As salinity increases with sea-level rise, marsh habitats will convert to communities dominated by more salt-tolerant plant species (Sharpe & Baldwin, 2012; Warren & Niering, 1993). Moreover, anthropogenic restrictions to upslope migration (Enwright, Griffith, & Osland, 2016), in conjunction with sea-level rise, may result in the expansion of saltmarshes at the expense of other wetland types, yielding an overall shift to more saline conditions (Visser, Duke-Sylvester, Carter, & Broussard, 2013). Changes in wetland ecosystem structure may eventually reflect altered ecological function and ecosystem services. In tidal freshwater forested wetlands impacted by sea-level rise, the transition to herbaceous oligohaline marsh resulted in greater nitrogen and phosphorus mineralization fluxes and turnover (Noe, Krauss, Lockaby, Conner, & Hupp, 2013). Similarly, the transition of herbaceous saltmarsh to mangrove forest significantly altered ecosystem function, with greater carbon sequestration rates and lignin storage rates in mangroves compared to saltmarshes (Bianchi et al., 2013).

Coastal wetlands provide numerous ecosystem services (Barbier et al., 2011), including significant carbon storage in living and non-living biomass and in flooded soils (McCleod et al., 2011). Furthermore, unlike terrestrial soils that may become carbon-saturated over time (Stewart, Paustian, Conant, Plante, & Six, 2007), coastal wetlands continually accrete mineral sediments and organic matter to keep pace with sea-level rise (Reed, 1995); thus, the potential for carbon storage in wetland soils increases over time (Chmura, Anisfeld, Cahoon, & Lynch, 2003).

Carbon storage in wetlands is the net result of organic matter production and organic matter loss, for example, decomposition.

Decomposition of organic matter is influenced by internal and external drivers (Godshalk & Wetzel, 1978). When considering the effect of an ultimate driver, such as sea-level rise, on organic matter decomposition, internal and external drivers will have indirect and direct impacts, respectively, on the fate of organic matter. Internal drivers are characteristics of the organic matter itself and include qualities of plant morphology and chemical composition of the plant material (McKee & Seneca, 1982; Melillo, Naiman, Aber, & Linkins, 1984). In contrast, external drivers of decomposition are characteristics of the environment and include soil microbe and detritivore community composition (Morrisey, Berrier, Neubauer, & Franklin, 2014; Valiela et al., 1985) and abiotic conditions, such as soil temperature, flood duration and frequency, and salinity (Reddy & Patrick, 1975; Weston, Dixon, & Joye, 2006). Therefore, sea-level rise has the potential to impact organic matter decomposition indirectly, by forcing shifts in plant community composition and litter quality (internal controls), and directly, through altering salinity and flooding (external controls) (Stagg, Schoolmaster, Krauss, Cormier, & Conner, 2017). Furthermore, these indirect and direct impacts are resolved at different spatial and temporal scales (Herbert et al., 2015; Neubauer, Franklin, & Berrier, 2013); therefore, it is critical that we quantify both internal and external controls on organic matter decomposition, if we hope to accurately predict the fate of organic matter in a future with sea-level rise.

Although there has been much recent progress in elucidating fine-scale mechanisms of soil respiration in response to elevated salinity (Chambers, Osborne, & Reddy, 2013; Chambers, Reddy, & Osborne, 2011; Neubauer, 2013; Neubauer et al., 2013; Weston, Vile, Neubauer, & Velinsky, 2011; Weston et al., 2006), we still lack a comprehensive understanding of the mechanisms that control organic matter decomposition in coastal wetlands at the landscape scale (but see Janousek et al., 2017; Weston, Neubauer, Velinsky, & Vile, 2014). To address this, we measured decomposition of in situ litter and a standardized carbon source across a landscape-scale salinity gradient that incorporated changes in vegetation community to address the following research questions: (1) What drivers influence organic matter decomposition along a landscape salinity gradient in coastal marshes? (2) How do long-term, indirect, impacts of sea-level rise differ from short-term, direct, impacts of sea-level rise on organic matter decomposition?, and (3) What are the implications for long-term carbon storage in estuarine coastal wetlands impacted by sea-level rise?

2 | MATERIALS AND METHODS

2.1 | Study sites

Above- and below-ground decomposition was measured in estuaries along a landscape-scale (c. 65 km) salinity gradient that incorporated fresh (0–0.5 ppt), oligohaline (0.5–5 ppt), mesohaline (5–18 ppt) and polyhaline (>18 ppt) coastal marshes as defined by Cowardin, Carter, Golet, and LaRoe (1979) (Figure 1). Due to high temporal variation in salinity, wetland community types were defined not only by measured salinity but also by dominant vegetation species known to be associated with specific salinity and hydrological regimes (Visser, Sasser, Chabreck, & Linscombe, 2002). Fresh sites were dominated by *Panicum hemitomon* and *Typha latifolia*, oligohaline sites were dominated by *Sagittaria lancifolia* and *Schoenoplectus americanus*, mesohaline sites were dominated by *Spartina patens* and *S. americanus*, and polyhaline sites were dominated by *Spartina alterniflora* and *Juncus roemerianus*. Within each of the four wetland types, six replicate sites were established across two hydrologic basins, Terrebonne and Barataria Basins, for a total of 24 sites (Figure 1; Baustian et al., 2017; Stagg et al., 2017).

2.2 | Response variables

2.2.1 | Litter decomposition

Rates of above- and below-ground organic matter decomposition were measured using the litter bag technique (Hackney & de la Cruz, 1980), which integrates short- and long-term decomposition processes associated with labile and refractory organic matter (Valiela et al., 1985). Litterbags containing site-specific above-ground biomass and litterbags containing site-specific below-ground biomass, or litter, were installed in three replicate plots in each site. Live biomass of each site-specific dominant species was collected from a subset of sites within each wetland type and hydrologic basin (subset n = 8) in July 2014. Above-ground biomass of each dominant species was collected from a monospecific stand, clipped at the soil surface and sorted into live and dead pools upon returning to the laboratory. To

collect below-ground biomass in large quantities, 20-cm wide × 30cm deep sods were harvested from monospecific stands representing each dominant species. The sods were transported back to the laboratory, where the below-ground biomass was rinsed over a 1-mm sieve to remove soil particles. The remaining macro-organic matter was separated into live and dead components. Live roots and rhizomes were distinguished from dead roots and rhizomes by colour, turgidity and structural integrity (Schubauer & Hopkinson, 1984). Above- and below-ground live biomass was allowed to air-dry to a constant mass for at least 1 week before placement in litterbags. Live, air-dried, litter was used in place of senesced litter to capture weight loss associated with initial decay processes, such as leaching, that would have already occurred in senesced material collected from the field (McKee & Seneca, 1982). Above-ground litterbags were prepared by filling mesh bags (20 cm long × 20 cm wide × 1.5 mm opening) with live air-dried leaf and stem material (20 g/bag). Below-ground litterbags were prepared by filling mesh bags (8 cm long \times 20 cm wide \times 1.0 mm opening) with live air-dried roots and rhizomes (5 g/bag). Generally, aboveground litter bags have a larger mesh opening than below-ground litterbags (Halupa & Howes, 1995; Hemminga, Kok, & de Munck, 1988), to allow for the passage of small and young invertebrates (McKee & Seneca, 1982). A subsample of the initial air-dried material for each species was weighed, oven-dried at 60°C and reweighed to calculate a moisture correction factor, which was applied to the starting mass (w_0) of air-dried litter used in subsequent calculations.

Above- and below-ground litterbag transects were established perpendicular to the water body and included three replicate plots located 10, 25 and 40 m from the shoreline. Above-ground litterbags were secured on the soil surface with landscape pins, and belowground litterbags were inserted into the soil to a depth of 10 cm. Four litterbags were installed in each replicate plot in October 2014 (n = 288 above-ground litterbags, n = 288 below-ground litterbags),



FIGURE 1 Decomposition study sites located along a landscape-scale salinity gradient spanning four wetland types in coastal Louisiana, USA

and individual litterbags were retrieved from each plot at four intervals (1, 3, 6 and 12 months after installation) to follow a model of exponential decay. After retrieval, the above- and below-ground litter bags were gently rinsed with deionized water over a 1-mm sieve, and remaining litter was oven-dried for at least 48 hr to a constant mass at 60°C (Halupa & Howes, 1995). The litter was then weighed and retained for further chemical analyses. Per cent mass remaining (% MR) was calculated using the following equation:

% MR = (w_t/w_0) × 100

where w_0 is dry weight at time zero, and w_t is dry weight at time t (days after installation).

The proportion of mass remaining over time was used to estimate two parameters that describe the decomposition process: (1) the decay rate, or exponential decay constant, and (2) the asymptote, or non-decomposable fraction. The exponential decay constant was derived using a single negative exponential decay model:

$$X = e^{-kt}$$

where X is per cent mass remaining after time, t (days after installation) and -k is the instantaneous decay constant (per day) (Weider & Lang, 1982). Additionally, we used an asymptotic model to estimate the non-decomposable fraction, or asymptote:

$$X = C_a + (1 - C_a)e^{-k_a t}$$

where C_a is the asymptote, or fraction of material remaining (%; Weider & Lang, 1982). Because the single exponential decay model provided a better fit for decay constant estimates, we only used the asymptotic model to estimate asymptotes, not decay constants.

2.2.2 | Cellulose decay

In addition to litter decomposition, we also measured cellulytic activity using the cotton strip technique, which provides a measure of shortterm loss of labile carbon (Maltby, 1988). Cotton strips are made from artist canvas which is comprised of 98% holocellulose, and by using a standardized carbon source, we were able to isolate external factors that influence microbial activity (Mendelssohn et al., 1999; Slocum, Roberts, & Mendelssohn, 2009).

Cotton strips were installed in three replicate plots along a transect parallel to the litterbag transects. Below-ground cotton strips (10-cm wide × 30-cm long) were inserted vertically into the soil to a depth of 25 cm. The cotton strips were deployed four times seasonally and retrieved after 12–14 days in the soil depending on the water surface temperature (Slocum et al., 2009). Above-ground cotton strips (20 cm × 20 cm) were deployed in October 2015, secured to the soil surface using landscape pins and retrieved 14 days later. Three cotton strips (two test strips and one reference strip) were placed in each replicated plot. Reference strips, used to quantify the tensile strength of non-decomposed material, were handled exactly the same as the test strips, but retrieved immediately after deployment.

After retrieval, cotton strips were rinsed gently with deionized water to remove all soil and extraneous material, and the cotton strips were allowed to air-dry for at least 48 hr. Cotton strips were cut into 2-cm substrips along the vertical profile, and decomposition of the 2-cm substrips was measured as tensile strength lost, compared to the reference substrip, using a Dillon Quantrol[™] Snapshot Tension Compression Motorized Test Stand tensometer connected to a Dillon Quantrol[™] Advanced Force Gauge (Slocum et al., 2009). Cellulose decay rate was calculated as per cent cellulose tensile strength lost per day (% CTSL per day):

% CTSL per day = $[1 - (T/R) \times 100]/t$

where T is the force (N) required to tear the test substrips, R is the force (N) required to tear the reference substrips and t is time (days) in the marsh.

2.3 | Predictive variables

2.3.1 | External drivers

All study sites were located within the 1-km² boundary of a Coastwide Reference Monitoring Systems station (http://lacoast.gov/crms2/home.aspx), where surface water salinity and surface water elevation are measured hourly. Marsh surface elevation of 15 plots within each site (*n* = 360) were surveyed using Real Time Kinematic methodology (Gao, Abdel-Salam, Chen, & Wojciechowski, 2005) with a Trimble R10 GNSS System (Trimble Navigation Limited, USA; Chen et al., 2011) and rectified to the North American Vertical Datum of 1988 (NAVD88) using Trimble Business Center 2.5 software for data post-processing (Trimble Navigation Limited, USA). We used marsh elevation data in conjunction with surface water elevation data to calculate flood depth and duration for each of 15 plots in each site.

Discrete soil and porewater samples were taken to measure a suite of environmental parameters in December 2014. At each site, two soil cores (10-cm diameter × 30-cm length) were collected near each of the three replicated plots along the below-ground litterbag transect (n = 72). After collection, the soil cores were sectioned into two increments (0–15 cm and 16–30 cm) and immediately placed on ice in the field and transported back to the laboratory, where they were homogenized. The first core was used for analysis of soil bulk density (Blake, 1965), % moisture (Blake, 1965), % organic matter (Oliver, Lotter, & Lemcke, 2001) and electrical conductivity (EC; Rhodes, 1996).

The second soil core was used to measure soil pH (Thomas, 1996), soil total C, N and P, soil extractable nutrients (PO_4 -P and NH_4 -N) and other elements of interest (Ca, Cu, Fe, K, Mg, Na, Ni, P). The homogenized soil was dried to a constant weight at 60°C, ground in a Wiley Mill (Model #4, 20 mesh; 850 µm) and separated into several scintillation vials for multiple analyses. Soil total N and total C were measured using a Costech[®] 4010 Elemental Combustion analyzer (Nelson & Sommers, 1982; EPA Method 440). Extractions were performed for the following analyses: soil total P (HCl, Aspila, Agemian, & Chau, 1976), PO_4 -P (Bray-2, Olsen & Sommers, 1982), NH_4 -N (KCl, Keeney & Nelson, 1982), and other parameters of interest (H_2NO_3 , American Public Health Association, 2005a). Soil total P, PO_4 -P samples and NH_4 -N were measured on a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA; EPA Method 365.5; EPA Method 350.1). The remaining extracts were analysed with an inductively coupled argon plasma optical emission spectrometer (ICP-OES) (Varian-MPX, Agilant, USA; American Public Health Association, 2005b).

Simultaneously, four separate aliquots of porewater were collected from a depth of 10 cm using the sipper-tube method (Vasilas & Vasilas, 2013). One aliquot of water was used to measure porewater pH (EPA Method 150.1) and salinity (EPA Method 120.1). The second porewater sample was used to measure porewater total N and total P following persulfate oxidation (D'Elia, Steudler, & Nathaniel, 1977; Ebina, Tsutsui, & Shirai, 1983) on a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA). The third aliquot was filtered through a 0.45-µm filter to measure NH₄-N, and PO₄-P using a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA; EPA Method365.5; EPA Method 350.1). The fourth aliquot was first filtered (45 µm) and then acidified to pH <2 to measure other elements of interest using an inductively coupled argon plasma optical emission spectrometer (ICP-OES) (Varian-MPX, Agilant, USA; American Public Health Association, 2005b).

2.3.2 | Internal drivers

Above- and below-ground biomass from each wetland type along the salinity gradient was collected to characterize chemical composition of the litter in July 2013 and 2014. In July 2014, subsamples of initial above- and below-ground air-dried biomass collected for each relevant dominant species within each wetland type were analysed for lignin content using the acid-detergent fibre and acid-insoluble ash techniques (Van Soest & Wine, 1968). Because insufficient initial biomass remained for further analyses, separate vegetation samples, previously collected from the study sites and analysed for total C and total N in July 2013, served as a proxy for the litter used in the litterbags. In July 2013, above-ground biomass was clipped at the soil surface from 0.25-m² quadrats, separated into total live and total dead components, and weighed after drying to a constant mass at 60°C (Mendelssohn, 1979). After above-ground biomass was removed from the plot, a sharpened 10-cm PVC corer was used to collect below-ground biomass from the centre of the quadrat. The cores were taken to a maximum depth of 30 cm, or the entire root mat thickness and were washed in a 1-mm sieve to remove soil particles. Live roots and rhizomes were separated from dead roots and rhizomes and the remaining matrix of dead organic material based upon biomass colour, turgor and buoyancy (Schubauer & Hopkinson, 1984). All material was dried at 60°C to a constant mass, and weighed. Above- and below-ground vegetation samples were then ground in a Wiley Mill (Model #4, 20 mesh; 850 µm), oven-dried at 60°C and analysed for total C and total N using a Costech® 4010 Elemental Combustion analyzer (Nelson & Sommers, 1982; EPA Method 440). Only values for live biomass samples were used in subsequent statistical analyses.

2.4 | Statistical analysis

We used a nonlinear regression to estimate decay constants and asymptotes from single exponential decay models and asymptotic models respectively. Nonlinear regression models were developed for each plot in each site (above-ground n = 72, below-ground n = 72). Only estimates from models that successfully converged were used in subsequent statistical tests. We used a mixed-model ANOVA with a randomized complete block design with sampling to compare variation in response variables (decay constants, asymptotes, cellulose decay rates). The fixed effect of wetland type was the treatment effect, basins represented error associated with blocking and three sites within each basin by wetland type treatment combination represented site-level error. Response variables were measured in three plots within each site, which represented sampling error. Principal component analysis (PCA) was used to explain variation in the environmental parameter dataset, and an analysis of similarity (ANOSIM) was performed to determine whether the principal components (PCs) varied significantly among the treatment groups (wetland type). We calculated correlation coefficients to measure the linear association between redox potential and PC factor scores. Finally, we performed multiple linear regression analysis using the Im function to identify significant predictors of decomposition. For each response variable, we identified a full model a priori that included explanatory variables of known importance and relevance. The litter decomposition models predicted above- or below-ground litter decomposition rate as a function of litter quality, soil and porewater physico-chemistry, and flooding. The cellulose decay models predicted above- or below-ground cellulose decay rate as a function of soil and porewater physicochemistry and flooding. We used principal component factors as explanatory variables to represent porewater and soil physico-chemistry and flooding. Because not all litter quality parameters were significantly correlated with a principal component, we included litter lignin and nitrogen content as explanatory variables in the multiple regression analyses using the observed data in place of the factor scores. The following analyses were performed in SAS 9.3 software (SAS Institute Inc, 2011): nonlinear regression (proc nlin), ANOVA (proc mixed) and correlation analysis (proc corr). The following analyses were performed using R software (R Development Core Team, 2013): PCA, ANOSIM and multiple linear regression.

3 | RESULTS

3.1 | Response variables

3.1.1 | Litter decomposition

In all wetland types, above- and below-ground litter significantly declined with time (Table 1, Figure 2). There was a significant interaction between above- and below-ground decay rate and wetland type (p = .0004, df = 3, F = 6.46); however, regardless of wetland type, above-ground litter decomposed faster than below-ground litter. In both above- and below-ground litter pools, the decay rate was greatest

Wetland type	Pool	Parameter	Estimate	SE	t-value	p-value
Fresh	Above	k	0.003	9.10E-05	32	<.0001
Oligohaline	Above	k	0.005	0.00041	13.1	<.0001
Mesohaline	Above	k	0.003	0.00012	20.8	<.0001
Polyhaline	Above	k	0.004	0.00012	33.7	<.0001
Fresh	Below	k	0.002	0.00011	15.6	<.0001
Oligohaline	Below	k	0.003	0.00024	12.9	<.0001
Mesohaline	Below	k	0.001	0.0001	12.8	<.0001
Polyhaline	Below	k	0.001	0.0001	13.3	<.0001
Fresh	Above	а	21.99	6.27	3.51	0.0008
Oligohaline	Above	а	23.02	5.43	4.24	<.0001
Mesohaline	Above	а	21.97	7.11	3.09	.003
Polyhaline	Above	а	7.67	9.41	0.82	.42
Fresh	Below	а	44.13	6.27	7.04	<.0001
Oligohaline	Below	а	31.85	5.21	6.11	<.0001
Mesohaline	Below	а	61.74	5.43	11.37	<.0001
Polyhaline	Below	а	44.18	5.95	7.43	<.0001

TABLE 1 Nonlinear regression estimates of single exponential decay constants (-*k*, per day) and asymptotes (a, %) for above- and below-ground litter decomposition

in the oligohaline marsh. In the above-ground litter pool, decay rate in the polyhaline marsh was significantly greater than decay rates in the fresh and mesohaline marshes (Figure 2a). In contrast, below-ground litter decay rates did not vary significantly among the fresh, mesohaline and polyhaline marshes (Figure 2b).

There was a significant interaction between above- and belowground asymptotes and wetland type (p = .0356, df = 3, F = 3.04, Figure 2). Above-ground litter decomposition was more complete (smaller asymptote) than below-ground litter decomposition in all wetland types, with the exception of the oligohaline marsh, where they were equivalent. Within the above-ground litter pool, there was no significant variation in the fraction of litter remaining among the four wetland types (Figure 2a). In contrast, below-ground, the fraction of litter remaining was significantly higher in the mesohaline marsh compared to all other wetland types (Figure 2b).

3.1.2 | Cellulose decay

Cellulose decay was greater below-ground than above-ground (Figure 3). Furthermore, trends in cellulose decay along the landscape salinity gradient were different between above- and below-ground pools (p = .002, df = 3, F = 4.88). Above-ground cellulose decay was greatest in the polyhaline marsh, but otherwise similar among the other wetland types. Below-ground cellulose decay significantly increased along the gradient from fresh to polyhaline marsh.

Additionally, there was a significant interaction between wetland type and depth (p < .0001, df = 42, F = 3.98; Figure S1). At the surface, cellulose decay rates were similar along the landscape gradient. As depth below the soil surface increased, there was a divergence in cellulose decay among the wetland types, and overall rates of decay were greater in the mesohaline and polyhaline marsh as compared to the fresh and oligohaline marsh.

3.2 | Predictive variables

The PCA generated three PCs that cumulatively explained 59% of the variance in the predictive variable dataset (Table S1). The first PC (PC1-Physico-chemical) explained 39% of the variance and was defined by porewater and soil physico-chemical properties including temperature, salinity and nutrient parameters. Annual surface water temperature was positively associated with PC1 (R^2 = .65), as were porewater and soil salinity parameters such as porewater and soil EC $(R^2 = .90 \text{ and } .89 \text{ respectively})$. Soil nutrient parameters such as soil total nitrogen and total phosphorus were negatively correlated with PC1 (R^2 = -.90 and -.67 respectively). The second PC (PC2-Lignin) explained c. 13% of the variation and was defined by lignin content of above-ground (leaf) and below-ground (root) litter. Leaf lignin content was positively correlated with PC2 ($R^2 = .55$), and root lignin content was negatively correlated with PC2 ($R^2 = -.55$), whereas leaf and root litter nitrogen content were not significantly correlated with this or any other PC.

The third PC (PC3–Flooding) explained 7% of the database variance and was defined by elevation and flood duration parameters. Wetland surface elevation was negatively correlated with PC3 ($R^2 = -.55$), and annual per cent time flooded was positively correlated with PC3 ($R^2 = .54$).

There was a separation among the wetland types along both the PC1 (Physico-chemical) and PC2 (Lignin) axes (R = .212, p = .001 and R = .092, p = .001 for PC1 and PC2 respectively). As expected, the four wetland types separated by salinity (Figure 4a,b). Additionally, wetlands types with high leaf lignin content also had low root lignin content (Figure 4a,c).

Due to missing redox potential data, this parameter was not included in the PCA or in the subsequent multiple regression analyses. However, redox potential varied significantly among the wetland



FIGURE 2 Estimates of (a) aboveground litter decay constants and asymptotes along the landscape gradient and (inset) relative above-ground biomass remaining over time, (b) below-ground litter decay constants and asymptotes along the landscape gradient and (inset) relative below-ground biomass remaining over time. Bars represent means (n = 18), and error bars represent SEs. Capital letters denote statistical significance of post-hoc multiple comparisons among asymptote means from both above- and belowground pools. Lowercase letters denote statistical significance of post-hoc multiple comparisons among decay constant means from both above- and below-ground pools (Fisher's Protected LSD, $\alpha = 0.05$)

types and was highest in the fresh marsh and lowest in the mesohaline and polyhaline marshes (p < .0001, df = 3, F = 52.82; Figure 5). Additionally, redox potential was highly correlated with several wellcharacterized parameters associated with PC1 (Physico-chemical) such as porewater EC and porewater sulphur ($R^2 = -.63$, p < .0001; $R^2 = -.46$, p = .002 respectively).

3.3 | Multiple regression analysis

Initial nitrogen content was the only significant predictor of aboveground litter decomposition (Table 2), which increased with increasing litter nitrogen content (Figure 6a). Initial lignin content was a significant predictor of below-ground litter decomposition (Table 2), which declined with increasing lignin content (Figure 6b).

Neither PC1 (Physico-chemical) nor PC3 (Flooding) had a significant effect on above-ground cellulose decay (Table 2). In contrast, PC1 (Physico-chemical) and PC3 (Flooding) were important predictors of below-ground cellulose decay (Table 2), which increased with increasing salinity and flooding and decreasing soil nutrient concentrations (Figure 7a,b).

4 | DISCUSSION

To improve our understanding of how organic matter decomposition and the fate of carbon in coastal wetlands will be impacted by sea-level rise, we identified the internal and external drivers that influence decomposition in coastal wetlands across an estuarine salinity gradient spanning fresh to polyhaline wetland types. Internal drivers, such as litter quality, are characteristics of the organic matter itself, whereas external drivers, such as hydrologic conditions, are characteristics of the environment (Aerts, 1997; Webster & Benfield, 1986), and their effects on decomposition may be expressed through both direct and indirect pathways. For example,



FIGURE 3 Cellulose decay among different wetland types. Bars represent means (n = 540), and error bars represent SEs. Letters denote statistical significance of post-hoc multiple comparisons of means (Fisher's Protected LSD, $\alpha = 0.05$)

sea-level rise can impact soil organic matter decomposition indirectly through changes in internal drivers, such as plant community composition and litter quality, which control litter decay rate (Stagg, Schoolmaster, Krauss, et al., 2017). In this study, we found that, despite significant variation in environmental conditions along this gradient, external drivers, including porewater salinity and flood duration, had no significant predictive capacity for either above- or below-ground litter decomposition. Therefore, our results indicate that the indirect pathway mediated through changes in litter quality, an internal driver, was more important in controlling litter decomposition than direct effects of external drivers along this landscape gradient.

Previous research has documented variation in lignin content among different wetland plant species (Buth, 1987; Guo, Lu, Tong, & Guohua, 2008), and our measurements of litter lignin content for fresh, oligohaline, mesohaline and polyhaline species were similar to those reported in the literature (Table 3). However, decay constants from mixed-species litter material will differ significantly compared to litter comprised of a single species (Chapman, Newman, Hart, Schweitzer, & Koch, 2013). Therefore, in situ measurements of litter mixtures that represent the vegetation community are critical for achieving accurate estimates of litter decay and identifying patterns of decomposition among different wetland types.

Because lignin content can differ significantly between two species within the same wetland type or salinity zone, it is difficult to identify universal patterns of lignin content along a landscape-scale salinity gradient. Furthermore, changes in plant diversity along the landscape gradient may impact rates of decomposition. Odum (1988) observed greater plant diversity in fresh marshes compared to more saline marshes, which may affect the proportion of different species, and overall litter quality, in a litter mixture. Very few studies have compared litter quality and decomposition along a salinity gradient that incorporates changes in composition (Gallagher, Kibby, & Skirvin,





FIGURE 4 Principal Component Analysis biplots of observation projections, or factor scores, in component space for all comparisons between (a) principal component (PC) 1 and PC2, (b) PC1 and PC3, and (c) PC2 and PC3. In each plot, factor scores are coloured by wetland type. A subset of highly correlated vectors from each PC overlay the factor scores

1984; Lopes, Martins, Ricardo, Rodrigues, & Quintino, 2011; Scarton, Day, & Rismondo, 2002; Windham, 2001), and, as far as we know, this is the first study to quantify litter decomposition dynamics of different wetland types across the entire coastal marsh landscape salinity gradient. Odum's (1988) comparative review of fresh vs. polyhaline tidal marshes reports that freshwater macrophytes from the lower intertidal zone, such as *Sagittaria latifolia*, tend to have lower lignin content, higher nitrogen content and higher decay rates compared to



FIGURE 5 Variation in soil redox potential along landscape gradient. Box plot boundaries closest to zero represent the 25th percentile, the line within the boxes indicates the median, and boundaries farthest from zero represent the 75th percentile (n = 90). Whiskers indicate the 90th and 10th percentiles. Black dots represent outlying points. Letters denote statistical significance of post-hoc multiple comparisons of means (Fisher's Protected LSD, $\alpha = 0.05$)

polyhaline, or saltmarsh, species. In contrast, freshwater macrophytes from the upper intertidal, such as *T. latifolia*, more closely resemble typical saltmarsh plants in their lignin and nitrogen content and exhibit slower rates of decay than plants from the lower intertidal fresh zone. In support of Odum's conclusions, we found that litter decomposition was greatest in the oligohaline marshes, which were dominated by *S. lancifolia* and *S. americanus* and also had the lowest lignin content. The fresh marsh dominated by *T. latifolia* and *P. hemitomon* was similar in lignin content and decay rate to the mesohaline marshes dominated by *S. patens*, and the polyhaline marshes dominated by *S. alterniflora* and *J. roemerianus*. Thus, although landscape-scale salinity patterns of lignin content and litter decomposition are largely species-specific (Aerts & de Caluwe, 1997), it is clear that sea-level rise has the potential to alter the quality of carbon and indirectly impact decomposition along this gradient.

Similarly, initial litter quality, in the form of nitrogen content, was the best predictor of above-ground litter decomposition (Marinucci, Hobbie, & Helfrich, 1983; Taylor, Parkinson, & Parsons, 1989). Although some research identifies the ratio of lignin-to-nitrogen in initial litter quality as an important predictor of decomposition (Melillo. Aber, & Muratore, 1982; Valiela et al., 1984), our results indicate that only one of these variables was a significant predictor, either nitrogen content or lignin content, of above- or below-ground litter decomposition respectively. Likewise, a study by Melillo, Naiman, Aber, and Eshleman (1983) identified either lignin alone or in combination with nitrogen content as a significant predictor of decomposition. The significance of one predictor over another may be due to interactions between initial litter quality and environmental conditions. In general, if exogenous nitrogen (e.g. from soil or water column) is readily available to microbes, and/or initial litter lignin content is high, then initial litter nitrogen content may have little impact on decay rate (Melillo et al., 1982, 1984). Interestingly, despite these differences among aboveand below-ground litter content, the pattern of decay along the landscape gradient was similar, with the greatest decomposition occurring in the oligohaline marsh. Although salinity is a known regulator of plant nitrogen dynamics (Bradley & Morris, 1991; Morris, 1980), we did not observe a simple linear decline in litter quality with increasing salinity. Thus, it is clear that litter decomposition is controlled through an indirect pathway mediated by internal drivers, but more research is needed to identify the ultimate drivers that generate optimal litter quality for enhanced decay in the oligohaline marsh.

To characterize the direct effects of sea-level rise on decomposition, we controlled for the influence of litter quality by measuring the decay rate of a standard carbon source, cellulose, across the landscape-scale salinity gradient (Mendelssohn et al., 1999). Cellulose is a labile compound that rapidly decays during the initial phases of decomposition and serves as a readily available fuel for microbial activity

 TABLE 2
 Results of multiple linear regression analysis for litter decomposition and cellulose decay

Response variable	Predictive variable	Parameter estimate	SE	t-value	p-value	Model R ²
Above-ground litter	PC1	-1.77E-05	5.65E-05	-0.314	.755	.121
Decomposition	PC3	-4.95E-05	1.31E-04	-0.378	.707	
	LeafN	0.0003	1.04E-03	2.68	**.009	
	LeafLignin	-7.36E-05	2.18E-04	-0.338	.736	
Below-ground litter	PC1	4.31E-05	3.38E-05	1.27	.207	.395
Decomposition	PC3	5.07E-05	6.76E-05	0.750	.456	
	RootN	3.53E-04	3.13E-04	1.13	.265	
	RootLignin	-2.17E-04	3.63E-05	-5.98	***1.10E-07	
Above-ground	PC1	0.042	0.032	1.30	.198	.027
Cellulose decay	PC3	-0.021	0.075	-0.280	.780	
Below-ground	PC1	0.039	0.012	3.24	**.002	.195
Cellulose decay	PC3	0.066	0.028	2.36	*.021	

p* < .05; *p* < .01; ****p* < .001.



FIGURE 6 Linear regression of (a) above-ground litter decomposition and litter nitrogen content and (b) below-ground litter decomposition and litter lignin content. Fresh, oligohaline, mesohaline and polyhaline wetland types differentiated by shape symbols

(Hodson, Chrsitian, & Maccubbin, 1984). Therefore, in addition to identifying external controls on decay, we were also able to characterize the decomposition dynamics of the isolated labile carbon pool.

We found that below-ground cellulose decay increased with increasing salinity, which supports findings from recent studies that soil respiration is stimulated by salinity in short-term exposures that do not incorporate changes in carbon source (Chambers et al., 2011; Weston et al., 2006). While increasing salinity can have direct impacts on organic matter mineralization through altering the soil chemical composition and releasing previously soil-bound organic carbon (Dou, Ping, Guo, & Jorgenson, 2005), the pattern of cellulose decay along this salinity gradient was likely influenced by differences among the microbial communities (Chambers et al., 2013). As salinity continues to increase, sulphate reducers out-compete methanogens, and overall anaerobic metabolism is greater when sulphate is the dominant terminal electron acceptor (Sutton-Grier, Keller, Koch, Gilmour, & Megonigal, 2011; Weston et al., 2006).

In contrast to salinity, soil nutrients were negatively correlated with below-ground cellulose decay. Although Mendelssohn et al.



Increasing flooding

FIGURE 7 Linear regression of below-ground cellulose decay and (a) PC1 (Physico-chemical) and (b) PC3 (Flooding). Fresh, oligohaline, mesohaline and polyhaline wetland types differentiated by shape symbols

(1999) found that soil nutrients had a significant positive influence on cellulose decay in a *Phragmites australis*-dominated wetland, this trend is not universal among all wetland types. For example, the review by Rybczyk, Garson, and Day (1996) illustrates varying impacts of soil nutrients on soil organic matter decomposition. Even so, it is unlikely that high soil nutrients would directly inhibit cellulose decay. Rather, we propose that the stimulatory effect of elevated salinity and greater sulphate availability overcame the potential negative effects of low soil nutrient concentrations.

Flooding was also a strong predictor of decomposition, and had a direct positive effect on below-ground cellulose decay. Although greater flood duration can lead to anaerobic soil conditions (Gambrell & Patrick, 1978; Ponnamperuma, 1984), which can limit the rate of decomposition (Day & Megonigal, 1993; McKee & Seneca, 1982; White & Trapani, 1982), decomposition is not always slower under anaerobic conditions. For example, Kirwan, Langley, Guntenspergen, and

Species	Litter type	Lignin content (%)	Study
Typha latifolia	Leaves	12.2 ^L	Current study
		5.8 ^L	Moran & Hodson (1989)
		39.5-42.7 ^D	Welsch & Yavitt (2003)
		18.2 ^D	Poi de Neiff, Neiff, & Casco (2006)
	Roots	7.3 ^L	Current study
Panicum hemitomon	Leaves	6.4-7.3 ^L	Current study
		6.4 ^L	Moran & Hodson (1989)
		5.9 ^D	Osborne, Inglett, & Reddy (2007)
	Roots	8.8-12.2 ^L	Current study
Sagittaria lancifolia	Leaves	7.7-7.7 ^L	Current study
		18 ^U	Laursen (2004)
	Roots	5.4-7.4 ^L	Current study
		26 ^U	Laursen (2004)
Schoenoplectus americanus	Leaves	7.9-8.9 ^L	Current study
		20.5 ^D	Ball & Drake (1997)
	Roots	4.7-7.5 ^L	Current study
		14.43-26.50 ^L	Saunders, Megonigal, & Reynolds (2006)
Spartina patens	Leaves	7.8-9.2 ^L	Current study
		14.2 ^D	Ball & Drake (1997)
	Roots	14.8-18.6 ^L	Current study
		26.95-30.41 ^L	Saunders et al. (2006)
Juncus roemerianus	Leaves	9.9 ^L	Current study
		6 ^U	Benner et al. (1987)
	Roots	13.7 ^L	Current study
		5.1 ^U	Benner et al. (1987)
Spartina alterniflora	Leaves	5.5-5.7 ^L	Current study
		15.1 ^L	Maccubbin & Hodson (1980)
		13.1-16.8 ^L	Hodson et al. (1984)
		11.7 ^U	Wilson (1985)
		11-12 ^D	Wilson, Buchsbaum, Valiela, & Swain (1986)
		4.3-6.1 ^U	Benner et al. (1987)
	Roots	13.7-15.2 ^L	Current study
		12.2-19.3 ^U	Hodson et al. (1984)
		9.3 ^U	Benner et al. (1987)

TABLE 3 Litter lignin content of dominant species from each wetland type. Litter condition identified as live (L), dead (D) or unknown (U)

Megonigal (2013) observed a stimulatory flooding effect on root and rhizome decomposition. Furthermore, soil redox potential along this landscape gradient was more closely correlated with porewater salinity than with flood duration (Pw EC: $R^2 = -.62$, p < .0001; AnnFlood: $R^2 = -.39$, p = .01), indicating that the stimulating effect of flooding was not strongly associated with anaerobic conditions. Therefore, we propose that the positive relationship between flooding and cellulose decay illustrates the well-documented observation that microbial activity is moisture-limited (Frasco & Goode, 1982; Halupa & Howes,

1995; Newell, Arsuffi, & Palm, 1996; Reice & Stiven, 1983), at least in the top 20 cm of the soil profile. At further depths, cellulose decay below the soil surface was likely oxygen limited as soils become more reduced with increasing depth (Maltby, 1988; Schipper & Reddy, 1995). Similar to our findings, low oxygen availability has been identified as a primary inhibitor of cellulose decay at depths below 22 cm (Mendelssohn et al., 1999).

Surprisingly, none of the environmental drivers we measured had predictive capacity for above-ground cellulose decay. Although

above-ground cellulose decay varied significantly across the landscapescale salinity gradient (higher in polyhaline marsh), salinity per se was not a significant predictor of decay (sensu Mendelssohn et al., 1999). Several recent studies have illustrated that salinity can indirectly affect soil respiration through changes in microbial function, resulting in higher rates of carbon mineralization at higher salinities (Chambers et al., 2011; Neubauer, 2013; Sutton-Grier et al., 2011; Weston et al., 2006). Thus, we hypothesize that an unidentified mediating factor that varies with wetland type, such as microbial function (Capone & Kiene, 1988), is regulating cellulose decay. We suggest that future studies include focused measures of microbial structure and function along this landscape-scale gradient to confirm the mechanism of indirect effects of salinity on cellulose decay (Hopfensperger, Burgin, Schoepfer, & Helton, 2014; Morrisey et al., 2014; Neubauer, Givler, Valentine, & Megonigal, 2005).

In summary, our study showed that the indirect effect of sealevel rise on litter decomposition was mediated through changes in plant community composition and litter quality, which resulted in declining rates of litter decomposition along the gradient from oligohaline to polyhaline marshes. However, when we controlled for changes in litter quality, we found that increasing salinity and flooding stimulated decay of labile carbon (cellulose). We have identified two mechanisms of organic matter loss operating at different temporal scales that provide insight to the potential for long-term carbon storage as sea-level rises. Our results indicate that as sea level rises, initial direct effects of salinity will stimulate decay of labile carbon, but over time as vegetation community composition shifts to more saline wetland types, litter decay (decay of refractile carbon) will decline, yielding greater potential for long-term soil carbon storage through net accretion (Loomis & Craft, 2012). Recent studies have highlighted the importance of scale in considering the influence of sea-level rise on carbon loss from wetland systems (Herbert et al., 2015; Neubauer et al., 2013). Our research provides an example of how multiple mechanisms of carbon loss operating at different scales can yield different rates and patterns of organic matter decomposition, which is relevant not only in coastal wetlands but also in other ecosystems such as grasslands, shrublands and forests, where plant-mediated responses to climate change will have significant impacts on carbon dynamics (Jobbagy & Jackson, 2000).

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AUTHOR'S CONTRIBUTIONS

C.L.S., M.M.B. and C.L.P. conceived the ideas and designed methodology; C.L.S., M.M.B., C.L.P., T.J.B.C. and C.T.H. collected the data; C.L.S., M.M.B. and C.T.H. analysed the data; C.L.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All of the supporting data presented in this paper have been publically archived at sciencebase.gov: https://doi.org/10.5066/f7639mvk (Stagg, Baustian, Perry, Carruthers, & Hall, 2017).

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