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RESEARCH ARTICLE

Intrinsic and extrinsic drivers of organic matter processing along phosphorus and salinity gradients in coastal wetlands

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Abstract

1. Climate change is accelerating sea-level rise and saltwater intrusion in coastal regions world-wide and interacting with large-scale changes in species composition in coastal wetlands. Quantifying macrophyte litter breakdown along freshwater-to-marine coastal gradients is needed to predict how carbon stores will respond to shifts in both macrophyte communities and water chemistry under changing environmental conditions.
2. To test the interactive drivers of changing species identity and water chemistry, we performed a reciprocal transplant of four macrophyte litter species in seven sites along freshwater-to-marine gradients in the Florida Coastal Everglades. We measured surface water chemistry (dissolved organic carbon, total nitrogen and total phosphorus), litter chemistry (% nitrogen, % phosphorus, change in N:P molar ratio, % cellulose and % lignin as proxies for recalcitrance) and litter breakdown rates (k/degree-day).
3. Direct effects of salinity and surface water nutrients were the strongest drivers of k, but unexpectedly, litter chemistry did not correlate with litter k. However, salinity strongly correlated with changes in litter chemistry, whereby litter incubated in brackish and marine wetlands was more labile and gained more phosphorus compared with litter in freshwater marshes. Our results suggest that litter k in coastal wetlands is explained by species-specific interactions among water and litter chemistries. Water nutrient availability was an important predictor of breakdown rates across species, but breakdown rates were only explained by the carbon recalcitrance of litter in the species with the slowest breakdown (*Cladium jamaicense*), indicating the importance of carbon structure, and species identity on breakdown rates.
4. *Synthesis*. In oligotrophic ecosystems, nutrients are often the primary driver of organic matter breakdown. However, we found that variation in macrophyte breakdown rates in oligotrophic coastal wetlands was also explained by salinity and associated seawater chemistry, emphasising the need to understand how saltwater intrusion will alter organic matter processing in wetlands. Our results suggest that marine subsidies associated with sea-level rise have the potential to

accelerate leaf litter breakdown. The increase in breakdown rates could either be buffered or increase further as sea-level rise also shifts macrophyte community composition to more or less recalcitrant species.

KEYWORDS
carbon, coastal wetlands, lignin, litter decomposition, nitrogen, phosphorus, salinity, sea-level rise

1 | INTRODUCTION

Coastal wetlands make up less than 0.2% of the planet's ocean surface, but they account for 50% of total carbon (TC) burial in ocean sediments (Duarte et al., 2013). With climate change and land clearing for development reducing wetland areas world-wide (Salimi et al., 2021; Taillardat et al., 2020; Xi et al., 2021), understanding the drivers of organic carbon storage and dynamics within all wetlands, particularly in coastal wetlands, is essential (Schmidt et al., 2011). Sea-level rise is one of the major factors affecting carbon in coastal wetlands, as it changes organic carbon production, decomposition and movement (Chambers et al., 2015). For instance, mangrove expansion, driven by sea-level rise into and within coastal wetlands, is changing macrophyte communities and the storage of organic carbon in coastal ecosystems (Cavanaugh et al., 2014; Charles et al., 2020). Understanding patterns and magnitudes of changes in carbon storage requires quantifying direct (e.g., salinity increasing breakdown of organic matter) and indirect pathways (e.g., salinity changing plant communities, thus changing the quality of litter) through which different drivers alter organic matter breakdown in coastal wetlands (Stagg et al., 2018). In general, the breakdown of organic matter is mediated by microbes, invertebrates and leaching, each of which is in turn affected by the chemistry of its environments and the chemistry of the litter itself (Rejmánková & Houdková, 2006). Although much is known about specific drivers of organic matter breakdown in aerobic conditions, the influence of marine subsidies on organic matter processing in wetlands is uncertain and likely variable (Helton et al., 2015).

Coastal wetlands world-wide are undergoing climate-driven changes in species composition (Chen et al., 2011; Guo et al., 2017). As macrophyte communities change in coastal wetlands, the quality of litter being deposited is changing (Charles et al., 2020; Smith et al., 2019). Deposition of leaf litter plays an important role in the accretion of soil, especially in mangrove basins where thick layers of litter can contribute up to 3.4 mm of sediment accretion each year (McKee, 2011). At the same time, hydrologic pulses, due to increased water flow, or storm events can shift the distribution of litter, either accelerating downstream transport or pushing litter upstream with storm surge or tidal changes (Zhao et al., 2021). Shifting litter species and environmental drivers often alter the structure and function of microbial communities colonising litter, which drive rates of litter breakdown. Initial litter chemistry can determine the extent of microbial colonisation, which in turn drives further breakdown (Bärlocher & Kendrick, 1975; Cleveland et al., 2014). Lignin concentrations and stoichiometry (elemental ratios) play major roles in determining the initial quality of litter (Bradford et al., 2016; Hall et al., 2020; Melillo et al., 1982). Increases in lignin concentrations, even within different tissues of the same plant species, can decrease the quality of litter, making it more difficult to break down (Gallagher et al., 1984; McKee & Seneca, 1982).

Organic matter processing and nutrient cycling in coastal wetlands are changing with saltwater intrusion and sea-level rise (Tully et al., 2019). Intrusion of seawater acts as both a stressor and subsidy for microbial communities in coastal wetlands, commonly enhancing microbial processing of organic carbon (Chambers et al., 2016; Weston et al., 2011). Subsidies include alternate terminal electron acceptors, such as sulphur or iron, which can play an important role in enhancing anaerobic communities (Helton et al., 2015). In oligotrophic wetlands, phosphorus from seawater also subsidises nutrient-limited microbial communities (Kominoski et al., 2020; Servais et al., 2019). However, salinity from seawater can also act as a stressor to microbial communities, decreasing the breakdown rate of cellulose and decreasing the rates of denitrification (Mendelssohn et al., 1999; Neubauer et al., 2019).

At the same time, seawater intrusion is causing shifts in vegetation, changing the type and quality of litter being deposited (Charles et al., 2020). That change in quality plays a role in determining the limitations of wetland microbial communities (Stagg et al., 2018). Changing vegetation and mobilisation of stored carbon in the soil also change the composition of carbon in the water column (Bhattacharya & Osburn, 2020; Chen et al., 2013). Increases in bioreactive water column dissolved organic carbon (DOC) could create a priming effect, leading to an increase in the breakdown of recalcitrant DOC where there is available labile DOC (Guenet et al., 2010; Howard-Parker et al., 2020). Understanding both the direct and indirect effects of seawater intrusion is important for understanding what constrains microbial processing in different habitats, how litter of different qualities can ease those constraints, and how microbial communities under different limitations respond to changing litter quality.

Chemical differences among different species of litter influence the microbial communities that colonise it, and mixing litter types can lead to emergent communities based on the mixture (Chapman et al., 2013; Kominoski et al., 2009). Specific formation of litter microbial communities, and their specialisation within their own environment, can additionally lead to a home-field advantage for litter breaking down where it is normally produced (Kominoski et al., 2012; Yeung et al., 2019). Environmental chemistry is especially important in which it can reduce the stoichiometric mismatch between litter chemistry and decomposing microbes, making up for nutrients missing in the litter (Kominoski et al., 2015; Manning et al., 2015). The change in nutrients associated with colonisation by decomposing microbes often has the most significant effects on the worst quality litter, relative to environmental limitations (Cheesman et al., 2010; Suberkropp et al., 2010). Microbial communities can additionally be 'primed' to increase the breakdown of more recalcitrant material when more labile carbon is available in their environment (Guenet et al., 2010). Over time, microbial colonisation changes the quality of litter, making it more palatable to invertebrate consumers (Bärlocher & Kendrick, 1975), which further facilitates the invertebrate breakdown of litter (Graça, 2001; Motomori et al., 2001).

Our goal was to test the interacting drivers of changing species composition and environmental chemistry on organic matter processing and nutrient cycling. To achieve this, we performed a reciprocal transplant of different qualities of wetland macrophyte litter into novel environments across a gradient of salinity and phosphorus in coastal ecosystems. Here, we tested the following questions: (1) How does variation in litter chemistry across species interact with surface water physicochemistry to drive litter breakdown in coastal wetland ecosystems? (2) How does litter carbon recalcitrance (cellulose:lignin) and nutrient availability affect litter breakdown along freshwater to marine gradients? Our reciprocal transplant experiment explicitly tested the interaction between litter quality and the environment in freshwater, ecotone and mangrove wetlands in long- and short-hydroperiod wetlands, and in marine seagrass meadows of Florida Bay within the Florida Coastal Everglades. We predicted that litter chemistry (in terms of both phosphorus and carbon recalcitrance) would be a major driver of litter breakdown rates and that marine influences that alleviate anaerobic constraints would release both stoichiometric (with phosphorus subsidies) and redox constraint (with terminal electron acceptor subsidies) to increase breakdown rates in brackish and marine sites (Figure 1).

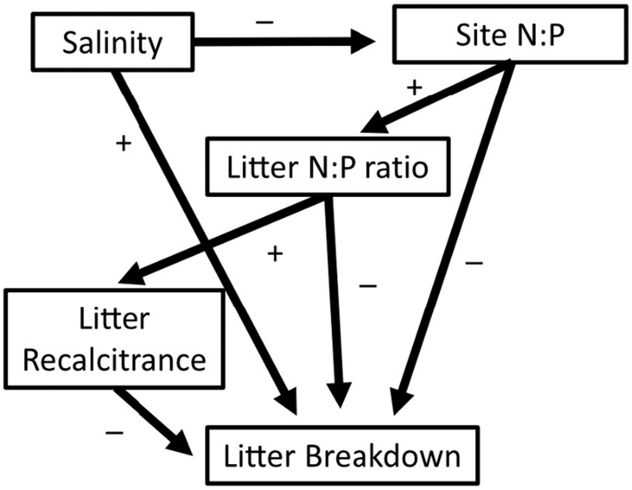

FIGURE 1 Conceptual model showing hypothesised drivers of leaf litter breakdown in P-limited oligotrophic coastal wetlands. + symbols indicate a positive relationship, while − symbols indicate a negative relationship. Litter recalcitrance refers to the ratio of cellulose to lignin in the litter.

2 | METHODS

2.1 | Site description and experimental design

Our study took place within Everglades National Park (Florida, USA) (Figure 2), an International Biosphere Reserve, a World Heritage Site and a Ramsar Wetland of International Importance. The Everglades begins at Lake Okeechobee in central Florida and flows from there to Florida Bay at the southern tip of the state. Everglades wetlands are highly oligotrophic and heterogeneous with wide variation in hydrology, productivity and relative nutrient limitation (Castañeda-Moya et al., 2013; Childers et al., 2003; Noe et al., 2001). The hydrology of the Everglades was radically altered starting in the early 1900s with the construction of drainage canals to create agricultural areas and to develop inundated areas (Light & Dineen, 1994). Under the Comprehensive Everglades Restoration Plan (CERP) and associated projects, one of the world's largest restoration projects, efforts are in place to restore sheet flow across the Everglades, which, among other changes, is shifting vegetation communities as legacy phosphorus is mobilised by restorative freshwater entering the system (Sarker et al., 2020). Legacy phosphorus has built up in different portions of the central and southern Everglades as a consequence of upstream farming around Lake Okeechobee. As a component of restoration efforts, a series of treatment wetlands have been created to prevent the movement of nutrients (especially phosphorus) from the farming areas and adjacent degraded wetlands to the Everglades wetlands further downstream (Sarker et al., 2020). Phosphorus is also entering the Everglades from the coast, because despite extremely low concentrations of phosphorus in the Gulf of Mexico (0.25–0.65 μmol/L), they are typically higher than that of the extremely oligotrophic wetlands further inland (Boyer, 2006; Fourqurean & Zieman, 2002). With this dynamic, sea-level rise is pushing more phosphorus into coastal wetlands, leading to shifts in vegetation communities (Charles et al., 2019, 2020; Childers et al., 2006). Both fresh and marine water contribute to changing phosphorus concentrations and vegetation communities. The combination of these shifting conditions and the robust data availability, due to monitoring by the Florida Coastal Everglades Long Term Ecological Research (FCE-LTER) programme, make the Everglades an ideal location to study how spatio-temporal variation in biogeochemistry affects the processing of organic matter as vegetation communities change.

Research was conducted at seven long-term sampling sites of the FCE-LTER programme: three along each of the two major drainages, Shark River Slough (SRS) and Taylor Slough/Panhandle (TS/

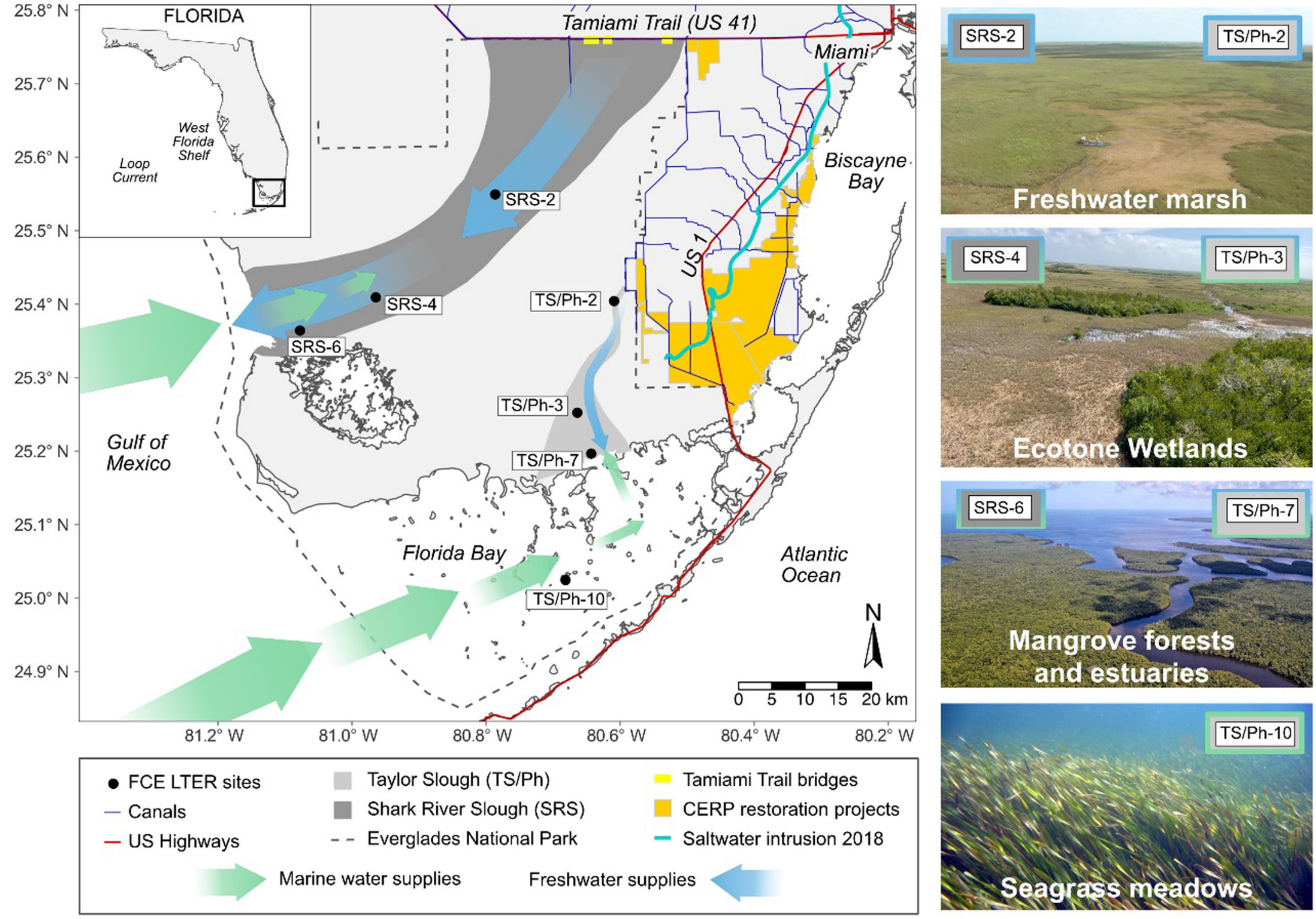

FIGURE 2 Location of study sites in the Florida Coastal Everglades (FCE), Everglades National Park (ENP), South Florida, USA. We deployed litterbags at marsh, ecotone and mangrove sites along the long-hydroperiod Shark River Slough (SRS-2, SRS-4, SRS-6), and the short-hydroperiod Taylor Slough (TS/Ph-2, TS/Ph-3, TS/Ph-7), and in a seagrass meadow in Florida Bay (TS/Ph-10). All sites are part of the FCE Long Term Ecological Research (FCE-LTER) programme. Each photograph represents an ecosystem type and is not necessarily indicative of a specific site.

Ph), and one in Florida Bay (Figure 2). For the Everglades, SRS is a high-productivity, long-hydroperiod wetland that transitions from sawgrass-dominated ridge and slough peat marshes to tidal riverine mangroves (Castañeda-Moya et al., 2013; Childers et al., 2006; Ewe et al., 2006). TS/Ph is a lower productivity (compared with SRS), short-hydroperiod wetland that transitions from sawgrass and periphyton-dominated marl prairies to microtidal mangrove scrub forests. We deployed litterbags at three sites (see Section 2.3 for details) in each drainage corresponding to freshwater (SRS-2, TS/Ph-2), ecotone (SRS-4, TS/Ph-3) and mangrove (SRS-6, TS/Ph-7). We also deployed bags at a single site in a seagrass meadow in Florida Bay (TS/Ph-10). All sampling was conducted under sampling permit EVER-2019-SCI-0055.

2.2 | Surface water physicochemistry

We used long-term data from monthly surface water grab samples for the period that litter was deployed at all sites to calculate the average concentrations of DOC, total nitrogen (TN), total phosphorus (TP), and salinity across the periods that litterbags were deployed (Briceño, 2020; Gaiser & Childers, 2021; Troxler, 2021; Troxler & Childers, 2021). Total phosphorus was measured following the method of Solórzano and Sharp (1980). Total nitrogen and DOC were measured using an Antek TN analyser (Antek Instruments, Houston, Texas, USA). DOC concentrations were measured using filtered water samples (0.7-µm GF/F filters; Whatman, Maidstone, UK) with a Shimadzu TOC Analyser (Shimadzu Corporation, Columbia, Maryland, USA). All water chemistry analyses were conducted at the Center of Research Excellence in Science and Technology (CREST) Center for Aquatic Chemistry and Environment (CAChE) Nutrient Core Facility that is NELAC Certified for non-potable water-General Chemistry under State Lab ID E76930. Surface water temperature was measured at the locations of gas flux towers for SRS-2, SRS-6, TS/Ph-1, TS/Ph-7 and TS/Ph-10. Missing data were estimated using water temperatures at the closest tower: Water temperature data at TS/Ph-1, SRS-6 and TS/Ph-7 were used as an estimate for TS/Ph-2, SRS-4 and TS/Ph-3, respectively.

2.3 | Litter breakdown rates and chemistry

Cladium jamaicense Crantz (sawgrass) and *Eleocharis cellulosa* Torr. (spikerush) are the dominant species in Everglades freshwater marshes, *Rhizophora mangle* L. (red mangroves) dominates at mangrove sites and coincides with higher salinity in estuarine habitats, and *Thalassia testudinum* Banks & Sol. ex. K.D. Koenig (seagrass) is the dominant species in the seagrass meadows of Florida Bay, which are fully marine. We collected litter to be deployed as live stems from SRS-2 (*C. jamaicense* and *E. cellulosa*), SRS-6 (*R. mangle*) and TS/Ph-10 (*T. testudinum*). Except for the seagrass, all litter was air-dried for at least 1 week and weighed prior to being sealed into litterbags. The seagrass litter was not dried, as drying can make it brittle and prone to rapid mass loss. The wet mass of seagrass was measured for each litterbag, and a subset of seagrass was oven-dried to calculate the ratio of dry to wet mass of litter deployed in each litterbag. All deployed seagrass was collected within 48 h of being deployed and was stored at 4°C until being deployed.

In December 2020, we deployed six fine and six coarse mesh litterbags on the soil surface at each of two replicate sub-sites for each site, that is, a total of $n=24$ litterbags of each species deployed to each site. We deployed litterbags with 3 g of air-dried litter of a single species, or the equivalent wet mass of *T. testudinum* inside both fine (1 mm) and coarse mesh (5 mm) bags with *C. jamaicense*, *R. mangle* or *E. cellulosa* litter at each of the seven sites, or *T. testudinum* at each mangrove site (TS/Ph-7, SRS-6) and in Florida Bay (TS/Ph-10). The fine mesh bags prevent macro-invertebrates from accessing litter, while the coarse mesh bags allow macro-invertebrates to access litter. We collected two litterbags from each subsite at 1, 4 and 10 months after deployment. Litter was rinsed with deionised water to remove sediment and oven-dried at 45°C for at least 3 days. After drying, the dry mass remaining was weighed and then ground using a ball mill. We calculated the ash-free dry mass (AFDM) for each sample by combusting a subsample at 550°C for 4 h and subtracting the ash mass remaining from the sample dry mass. We calculated degree-days to account for differences in temperature between sites as: degree-days = summed daily mean temperature °C for days deployed. We calculated the breakdown rate per degree-day (*k*/degree-day) for each sample as the negative slope of a regression of the natural log of the % AFDM remaining for each time point against degree-days for the period deployed (Follstad Shah et al., 2017; Woodward et al., 2012).

We measured per cent TN and TC for each litter sample from each time point using a CE Flash 1112 Elemental Analyser (City, State, Country). We measured per cent TP using a UV-2101 Shimadzu Spectrophotometer using a modified colorimetric method (Solórzano & Sharp, 1980). We analysed the recalcitrance of each litter sample with ramped pyrolysis. To do this, we combusted each sample at a series of thermal intervals associated with the loss of different qualities of carbon following Trevathan-Tackett et al. (2017): T1: 180°C (hemicellulose, carbohydrates and other labile carbon), T2: 300°C (refractory cellulose and carbohydrates) T3: 400°C (lignin and refractory carbon) and T4: 550°C (inorganic carbon). After each combustion, we measured the mass lost and the percentage of the remaining material that was carbon, using a CE Flash 1112 Elemental Analyser. We calculated the per cent TC lost at each thermal interval as: mass carbon post-combustion/mass of carbon pre-combustion × 100. We calculated the change in carbon fractions, TN, TP and TC as the difference between initial and both 4 and 10-month litter chemistry measurements. Our data can be accessed at the Environmental Data Initiative under package ID knb-lter-fce.1239.1 (Anderson & Kominoski, 2022).

2.4 | Data analyses

Principal component analysis was used to reduce the dimensionality of litter chemistry for the initial litter. We used both one and two-way analysis of variance (ANOVA) to test the effects of site and species on metrics of litter chemistry and breakdown rates, and Tukey HSD tests were used to test post hoc significance between groups. Linear regressions were used to test significant correlations between metrics of litter chemistry, site chemistry and breakdown rates. All analyses were performed using R version 4.2.0 (R Core Team, 2022). All plots were constructed with the 'ggplot2' package (Wickham, 2009).

We use path analysis to assess the hypothesised direct and indirect effects of environmental variables and litter chemistry on litter breakdown rates, using the 'lavaan' package in R (Rosseel, 2012). We constructed a hypothesised model using previous literature on how the interplay between site and litter chemistry determines the breakdown of litter (Bradford et al., 2016; Hall et al., 2020; Manning et al., 2015; Stagg et al., 2018). We used six predictor variables for litter *k*/degree-day, measured from both litter and site: Δlitter N:P ratio (change in litter N:P ratio from initial to 4 months), Δlitter cellulose:lignin ratio (change in cellulose to lignin ratio from initial to 4 months), surface water salinity, surface water TN:TP ratio, site as a factor and species as a factor. We used Δlitter N:P ratio and Δlitter cellulose:lignin ratio from 4 months as opposed to 10 because many samples at 10 months did not have sufficient material remaining for chemical analyses. We selected Δlitter N:P ratio as a measure of nutrient availability because the Everglades is highly phosphorus-limited (Childers et al., 2003). We used Δlitter cellulose:lignin ratio to represent changing recalcitrance of litter for the more recalcitrant fractions of carbon, while excluding inorganic carbon.

To better understand species-specific dynamics of litter breakdown, we constructed three sub-models using the same predictor variables for individual litter species *C. jamaicense*, *E. cellulosa* and *R. mangle*. We did not construct a sub-model for *T. testudinum* because we did not have adequate data points. For all models, we similarly evaluated model fit using the chi-squared test statistic and compared best-fit models based on Akaike's information criterion (AICc). We removed model links which were not significant and when it improved the model fit.

3 | RESULTS

3.1 | Surface water physicochemistry

Phosphorus concentrations in surface water were higher in SRS, than in TS/Ph, and Florida Bay had the lowest surface water TP (Table 1). Nitrogen concentrations in surface water were higher in the freshwater marsh of SRS, compared with TS/Ph. Nitrogen concentrations in the ecotone of TS/Ph were higher than SRS. Total nitrogen in the mangroves of TS/Ph was also higher than in SRS. Dissolved organic carbon was higher in SRS compared with TS/Ph and Florida Bay, but it was highly variable across sites (Table 1). Salinity significantly increased from freshwater to more marine sites and was significantly higher in SRS ecotone and mangrove sites than TS/Ph (ANOVA, $F_{(5,54)} = 38.86$, $p < 0.001$; Table 1). Temperature was not significantly different among sites (ANOVA, $F_{(5,54)} = 1.41$, $p = 0.24$; Table 1).

3.2 | Litter chemistry

We performed a principal component analysis of the metrics of initial litter chemistry using principal component analysis of seven measured parameters: TC, TP, TN and estimates of carbon quality measured by ramped pyrolysis: % hemicellulose, % cellulose, % lignin and % inorganic carbon (Figure 3). The first principal component explained 68% of the variation, primarily driven by % cellulose (20%), TP (18%) and TN (18%). The second principal component explained 19% of the variation and was primarily driven by % inorganic carbon (40%) and TC (24%). *R. mangle* and *T. testudinum* litter had higher average phosphorus (both with 0.11%) than *E. cellulosa* (0.03%) and *C. jamaicense* (0.003%) had the lowest.

Litter quality between species remained chemically distinct after 4 months of incubation; *R. mangle* and *T. testudinum* had significantly lower N:P ratios compared with *E. cellulosa* and *C. jamaicense* (ANOVA, $F_{(3,178)} = 5.79$, $p < 0.001$; Table S1). In the same period, both litter N:P ratios and carbon lability were significantly lower at marine sites compared with freshwater sites (ANOVA: $F_{(6,178)} = 26.87$, $p < 0.001$; and $F_{(6,175)} = 12.81$, $p < 0.001$, respectively; Table S1). In comparison with initial values, TP of *R. mangle* and *E. cellulosa* was unchanged, while phosphorus in *C. jamaicense* increased after 4 months of incubation at all sites, and *T. testudinum* lost phosphorus at all sites in those same 4 months (Table S1). In comparison with initial values, hemicellulose increases in all species, and, at brackish and marine sites (SRS-6, TS/Ph-7 and TS/Ph-10), the cellulose:lignin ratio decreased, indicating decreasing lability (Table S1).

There was a significant negative correlation between change in (Δ) litter N:P and salinity in all species: *C. jamaicense*, *E. cellulosa*, *R. mangle* and *T. testudinum* (Figure 4). There was a significant positive correlation between change in litter lability (Δcellulose:lignin ratio) and salinity in *E. cellulosa*, *R. mangle* and *T. testudinum*, but there was no significant correlation in *C. jamaicense* (Figure 4).

3.3 | Litter breakdown rates

There were significant effects of both site (ANOVA, $F_{(6,164)} = 10.08$, $p < 0.001$) and species (ANOVA, $F_{(3,164)} = 9.94$, $p < 0.001$) on the breakdown rate (*k*/degree-day) of litter over the course of 10 months, where *E. cellulosa* typically had the highest breakdown rates, and all species had significantly higher litter breakdown at the seagrass site TS/Ph-10 (Figure 5). We found no significant effect of mesh size on litter *k*/degree-day (ANOVA, $F_{(1,164)} = 1.875$, $p = 0.17$). There was a significant effect of salinity on *k*/degree-day for all four species: *R. mangle* ($R^2 = 0.40$, $p < 0.001$), *C. jamaicense* ($R^2 = 0.12$, $p < 0.05$), *E. cellulosa* ($R^2 = 0.33$, $p < 0.001$) or *T. testudinum* ($R^2 = 0.18$, $p < 0.05$). The high variability in both water column and litter chemistry makes it difficult to understand the dynamics affecting breakdown using ANOVA or regressions, so to better understand both direct and indirect effects of litter and site chemistry, we constructed a path analysis model of long-term rates of litter *k*/degree-day over the course of 10 months (Figure 6). The best-supported model predicted 20% of variation in leaf litter *k*/degree-day. Water column N:P ratio (−0.32) and salinity (0.67) were directly correlated with leaf litter *k*/degree-day (Figure 6). Salinity had indirect effects on litter *k*/degree-day through water column N:P (0.32; Table 2). Salinity (0.44) was correlated with the Δlitter recalcitrance (cellulose:lignin ratio) and Δlitter N:P ratio (−0.39), neither of which were significant drivers of leaf litter *k*/degree-day.

TABLE 1 Average (± SD) surface water physicochemistry data for the 10 months during which litter bags were deployed in marsh, ecotone and mangrove sites along the long-hydroperiod Shark River Slough (SRS-2, SRS-4, SRS-6), and the short-hydroperiod Taylor Slough (TS/Ph-2, TS/Ph-3, TS/Ph-7), and in a seagrass meadow in Florida Bay (TS/Ph-10).

Site name	Total nitrogen (μmol/L)	Total phosphorus (μmol/L)	Dissolved organic carbon (μmol/L)	Temperature (°C)	Salinity (PSU)
SRS freshwater	80.10 (19.14)	0.90 (0.28)	2003.25 (1304.13)	25.70 (2.68)	0.28 (0.08)
SRS ecotone	64.21 (9.48)	0.75 (0.15)	1857.05 (1413.42)	24.93 (3.01)	4.40 (4.44)
SRS mangrove	36.70 (8.12)	0.82 (0.11)	1077.50 (926.50)	24.93 (3.01)	25.76 (8.03)
TS/Ph freshwater	41.62 (5.46)	0.60 (0.16)	604.72 (58.19)	26.03 (3.24)	0.18 (0.03)
TS/Ph ecotone	86.93 (30.18)	0.72 (0.33)	866.57 (237.37)	27.07 (1.33)	0.25 (0.07)
TS/Ph mangrove	62.13 (8.99)	0.54 (0.09)	1006.02 (320.51)	27.07 (1.33)	10.64 (8.55)
TS/Ph seagrass	40.45 (11.08)	0.27 (0.05)	906.84 (940.51)	27.21 (2.54)	35.47 (4.64)

To better explain species-specific dynamics of litter breakdown, we constructed sub-models for *C. jamaicense*, *E. cellulosa* and *R. mangle*. The best-supported model for *C. jamaicense* explained 25% of variation in leaf litter *k*/degree-day (Figure S1). In the *C. jamaicense* model, there were direct effects of salinity (0.29), Δlitter recalcitrance (cellulose:lignin ratio; 0.28) and water column N:P (−0.26). Salinity had an indirect effect on leaf litter *k*/degree-day through water column N:P and Δlitter recalcitrance (cellulose:lignin ratio; Figure S1; Table S2A). The best-supported model for *E. cellulosa* explained 16% of the variation in leaf litter *k*/degree-day (Figure S2); salinity (0.40) had significant effects on litter *k*/degree-day. Salinity was also correlated with litter ΔN:P (−0.64), and litter recalcitrance (Δcellulose:lignin ratio; 0.72), which had no effects on leaf litter *k*/degree-day (Figure S2; Table S2B). The best-supported model for *R. mangle* explained 43% of variation in leaf litter *k*/degree-day (Figure S3); salinity (0.69) and water column N:P (−0.36) were both correlated with leaf litter *k*/degree-day. There were also indirect effects of salinity through its effects on water column N:P (0.35; Table S2C).

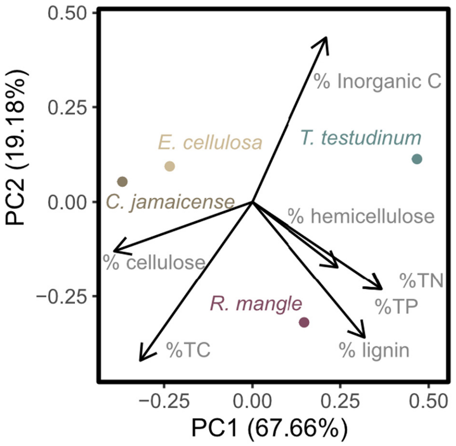

FIGURE 3 Principal component analysis of initial chemistry of four litter species prior to incubation. We constructed principal components from seven measured parameters: per cent carbon (%TC), per cent phosphorus (%TP), per cent nitrogen (%TN) and estimates of carbon quality measured by ramped pyrolysis: % hemicellulose, % cellulose, % lignin and % inorganic carbon. Colours indicate different species.

4 | DISCUSSION

Our goal was to understand how saltwater intrusion will affect the breakdown of litter as it changes available phosphorus, litter quality and other marine subsidies across coastal wetland habitats. Our results support salinity and nutrients as the major drivers of litter breakdown. There have been studies on how litter quality and decomposition vary along freshwater-to-marine gradients (Batistel et al., 2021; Lopes et al., 2011; Scarton et al., 2002; Stagg et al., 2018; Trevathan-Tackett et al., 2017). However, to our knowledge this study is the first to use reciprocal transplants of litter species along such gradients to investigate interactions among litter quality, breakdown and marine influence in highly oligotrophic coastal wetlands. We found that salinity and water column phosphorus availability played the biggest roles in determining the breakdown of litter, followed by litter phosphorus availability.

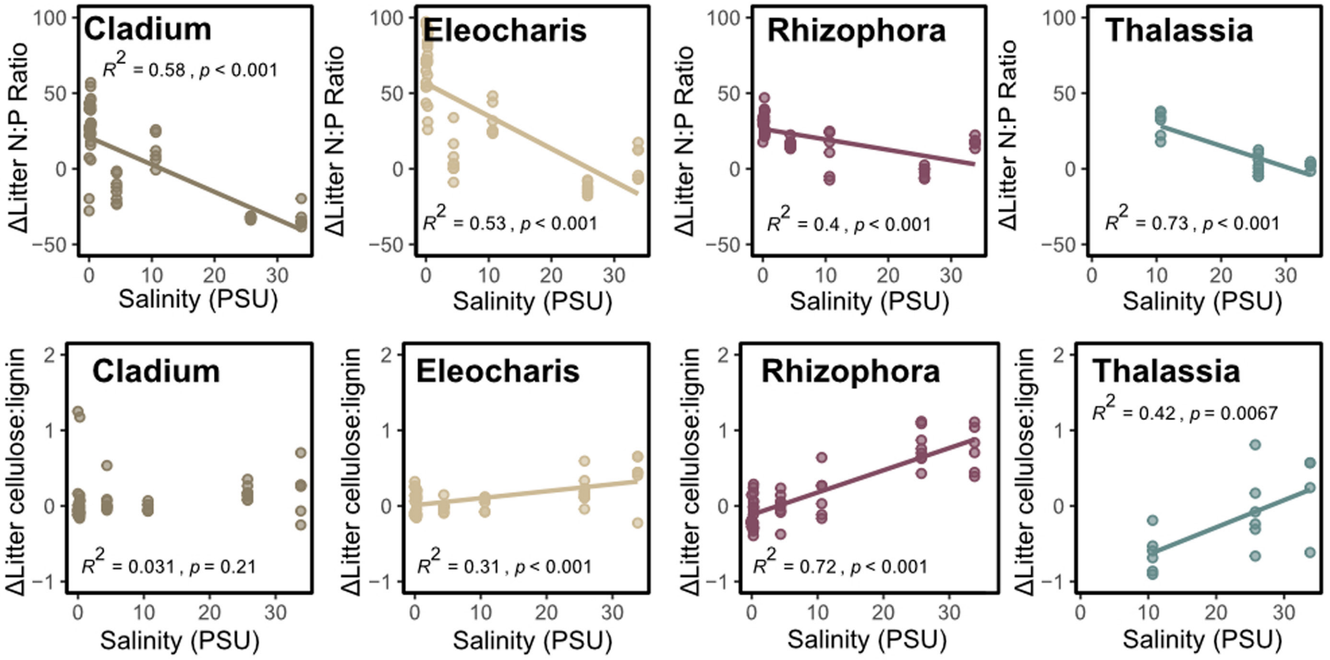

FIGURE 4 Linear relationships between average site surface water salinity and Δlitter N:P ratio and Δcellulose:lignin ratio after 4 months of incubation.

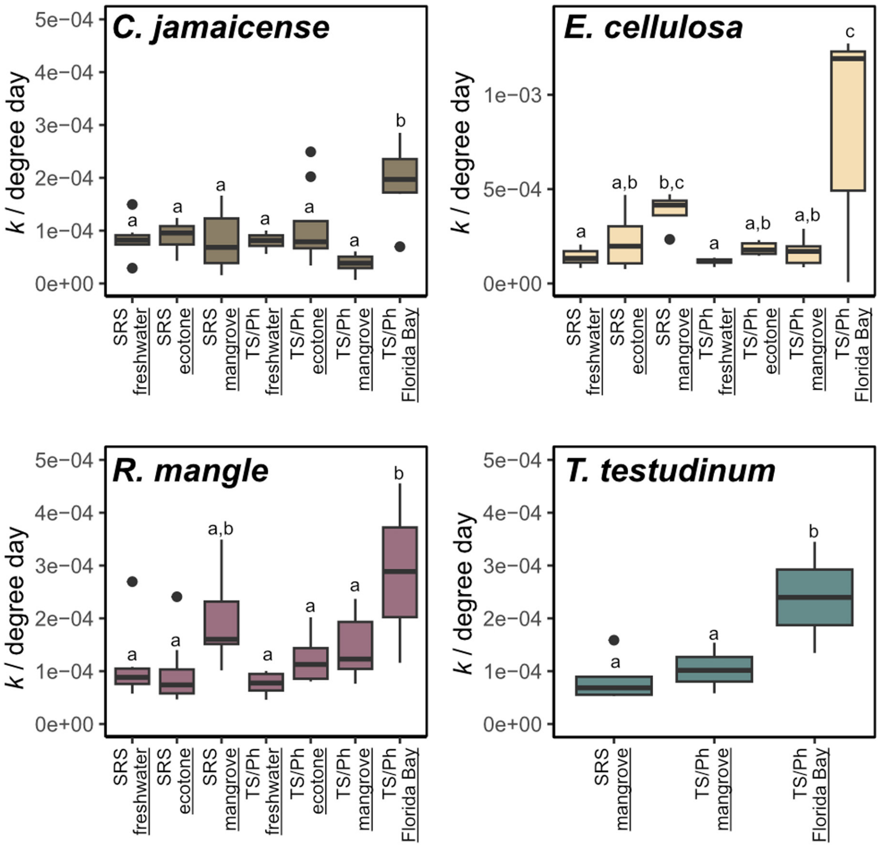

FIGURE 5 Litter breakdown rate: *k*/degree-day (summed mean daily temperature °C) after 10 months of incubation. We deployed litterbags at freshwater, ecotone and mangrove sites along the long-hydroperiod Shark River Slough (SRS-2, SRS-4, SRS-6), the short-hydroperiod Taylor Slough (TS/Ph-2, TS/Ph-3, TS/Ph-7), and in a seagrass meadow in Florida Bay (TS/Ph-10). Both mesh sizes were pooled for this plot as there was not a significant effect of mesh size. Letters indicate significant differences within a single panel, that is, among sites for each species, from a Tukey HSD test. Circles represent outliers with a value of more than 1.5 times the interquartile range.

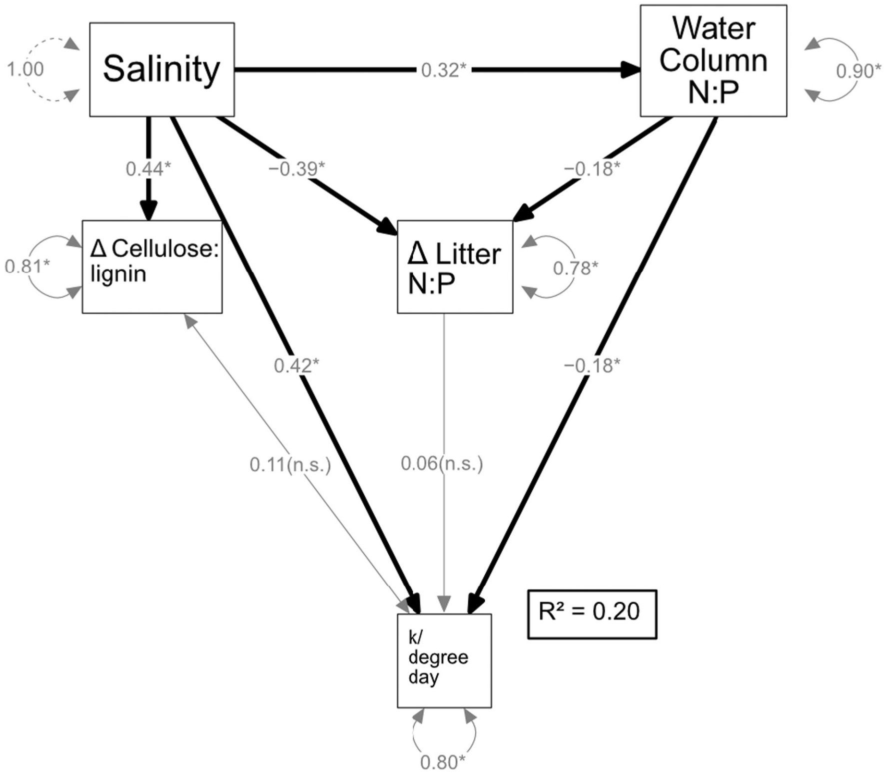

FIGURE 6 Best-supported model for 10-month litter breakdown (*k*/degree-day). Reported numbers are standardised path coefficients, where positive values indicate a positive relationship between variables. The best-supported model explains 20% of the variation in litter breakdown rates. Bolded arrows indicate significant path coefficients ($p < 0.05$). Dotted lines indicate significant correlations. Litter chemistry measurements from 4 months were compared with 10-month breakdown rates because many samples at 10 months did not have enough material remaining to measure chemistry.

Litter quality is often the most important factor influencing litter breakdown, with species-specific differences playing a bigger role than environmental variation (Guo et al., 2023; Lopes et al., 2011; Scarton et al., 2002; Stagg et al., 2018; Windham, 2001). In our study, we found large differences in breakdown rates between *E. cellulosa* and *C. jamaicense*, which are largely similar by our

TABLE 2 Effect coefficients for variables affecting litter *k*/degree-day after 10 months of incubation across seven sites in the Florida Coastal Everglades.

Variable	Direct effects	Indirect effects	Total effects
Salinity	0.42	−0.6	0.36
Water column N:P	−0.18	Not modelled	−0.18

measures of carbon recalcitrance. This difference suggests that chemical analysis of litter alone may not be sufficient to understand the recalcitrance of litter from different species and support studies showing that structural traits such as leaf toughness, and cuticle thickness may be more important to litter breakdown (Simões et al., 2021). Our sub-models showed that across all three species, salinity played the biggest role in determining breakdown rates, but species handled carbon recalcitrance differently. We found that only the species with the slowest breakdown rates (*C. jamaicense*) had a direct effect of change in litter recalcitrance on breakdown. This could indicate that a further understanding of microbial responses to litter mixtures (Chapman et al., 2013; Kominoski et al., 2009) will become increasingly important as vegetation communities change in response to sea-level rise and saltwater intrusion, especially where mangroves replace sawgrass (Charles et al., 2020; Smith et al., 2019).

Understanding litter quality and its effect on breakdown is important for predicting the effects of sea-level rise. Even infrequently pulsed salinity can have significant effects on the composition of litter, as it alters vegetation communities (Batistel et al., 2022; Birnbaum et al., 2021; Guo et al., 2023). We showed that changing vegetation communities can potentially drive significant differences in the breakdown of organic matter. In the Everglades, a shift from *Cladium jamaicense* to *Rhizophora mangle* is likely to lead to higher litter breakdown, but a more comprehensive understanding also requires an analysis of how net primary production and litter deposition rates will change in transition zones. The interaction between litter breakdown and salinity, through both indirect (changes to macrophyte species or growth rates) and direct (salinity effects on breakdown) pathways can lead to significant changes to the build-up and storage of blue carbon in coastal ecosystems (Cragg et al., 2020; Xia et al., 2021).

We found that salinity enhanced litter breakdown across all species and additionally modified environmental phosphorus availability. Without taking phosphorus availability into account, we did not see a strong effect of salinity, suggesting an interaction between phosphorus (as indicated by the path analysis approach) and salinity as drivers of breakdown. This finding supports previous studies that have shown salinity increasing the breakdown of litter (Frainer & Tiegs, 2022; Hu et al., 2019; Stagg et al., 2018; Trevathan-Tackett et al., 2021). Similarly, our data show that in addition to breakdown rates, salinity has a strong effect on the nutrient makeup of litter, even stronger than environmental chemistry, but breakdown rates were only affected by litter chemistry in a single species. Further study is needed to fully understand the mechanism driving these increases as there is little evidence that salinity itself (as opposed to seawater) is driving these changes (Martínez et al., 2020). Seawater can act as both stressor and subsidy depending on the local conditions, where marine subsidies of sulphate likely play an important role, especially where litter is deposited in largely anaerobic environments like the Everglades (Chambers et al., 2011; Weston et al., 2011; Zhang et al., 2023). Our study is one of the first ones to reciprocally transplant litter across a full range from fresh to fully marine water, showing clear differences between breakdown at ecosystem endmembers, as well as different drivers between species. This is important for understanding the effects of salinity because of the many conflicting factors that affect rates of breakdown including salt-stress interactions on both macro- and micro- decomposers where salinity is variable in the ecotone, as well as changing communities of microbial and invertebrate decomposers (Canhoto et al., 2017; Gómez et al., 2016; Tyree et al., 2016). We found little effect of mesh size on the breakdown of litter suggesting that in Everglades wetlands macro-invertebrates play only a minor role in the breakdown of litter. The lack of change in breakdown rates caused by mesh size indicates that salinity is specifically enhancing microbial breakdown of litter, and a limited effect of both litter phosphorus and carbon quality, in this highly phosphorus-limited and often anaerobic environment suggests that subsidies of alternate terminal electron acceptors such as iron or sulphates may be especially important drivers of litter breakdown.

5 | CONCLUSIONS

Sea-level rise and saltwater intrusion are rapidly changing the structure and function of coastal ecosystems world-wide. In coastal wetlands, changes in macrophyte species composition, litter deposition and rate of litter decomposition are affecting carbon storage (Charles et al., 2020; Kominoski et al., 2022). A holistic understanding of the drivers of organic matter processing is necessary to predict how accelerating sea-level rise will interact with shifts in species composition to affect carbon storage in coastal wetlands (Birnbaum et al., 2021). Our study contributes to that understanding, highlighting the importance of nutrient availability, carbon recalcitrance (through species-specific pathways) and salinity as key contributors to rates of litter breakdown, especially in highly oligotrophic wetlands. Our results suggest that direct measurements of litter chemistry may not be sufficient to understand the breakdown, and that structural traits are likely important. Increases in breakdown with higher salinity suggest that marine subsidies to decomposers are likely important drivers of litter breakdown where they are available. Additionally, our data suggest that marine subsidies transform litter chemistry, increasing its phosphorus content and making it more recalcitrant (likely as a result of breakdown). Understanding the drivers of organic matter processing in highly dynamic coastal wetland ecosystems is critical to preserving blue carbon stores in the face of sea-level rise (Cragg et al., 2020; Mcleod et al., 2011).

AUTHOR CONTRIBUTIONS

Kenneth J. Anderson, John S. Kominoski and Jay P. Sah participated in the writing and editing of this manuscript. Kenneth J. Anderson, John S. Kominoski and Jay P. Sah contributed to data analyses. Kenneth J. Anderson and John S. Kominoski collected data and designed the experiment.

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CONFLICT OF INTEREST STATEMENT

The authors report no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data from this research are archived through the Environmental Data Initiative (EDI): https://doi.org/10.6073/pasta/913c2e48833bd96849a4a7eb5f0571a8 (Anderson & Kominoski, 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Average (± SD) litter chemistry after 4 months of incubation in marsh, ecotone, and mangrove sites along the long-hydroperiod Shark River Slough (SRS-2, SRS-4, SRS-6), the short-hydroperiod Taylor Slough (TS/Ph-2, TS/Ph-3, TS/Ph-7), and in Florida Bay (TS/Ph-10).

Table S2: Effect coefficients for variables affecting litter *k*/degree-day for (A) *Cladium jamaicense*, (B) *Eleocharis cellulosa*, (C) *Rhizophora* *mangle* after 10 months incubation across seven sites in the Florida Coastal Everglades.

Figure S1: Best supported model for 10-month litter breakdown (*k*/degree-day) of *Cladium jamaicense*.

Figure S2: Best supported model for 10-month litter breakdown (*k*/degree-day) of *Eleocharis cellulosa*.

Figure S3: Best supported model for 10-month litter breakdown (*k*/degree-day) of *Rhizophora mangle*.

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