





## ARTICLE

## Coastal and Marine Ecology

## Coastal carbon processing rates increase with mangrove cover following a hurricane in Texas, USA

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## Abstract

Changes in species distributions and disturbances have complex impacts on ecosystem functioning. In many subtropical coastal wetlands, plant identity and cover are changing, as salt marshes dominated by low-stature herbaceous species transition to woody mangroves. These systems are also subject to frequent and potentially more intense hurricanes, which can alter a range of ecosystem structures and functions. We examined how changes in dominant plant species affected carbon processing in coastal wetlands following a hurricane. We experimentally manipulated cell-scale ( $3 \times 3$  m) cover of black mangroves (*Avicennia germinans*) and salt marsh plants (e.g., *Spartina alterniflora* and *Batis maritima*) in fringe and interior locations of 10 plots ( $24 \times 42$  m) to create a gradient in mangrove cover in coastal Texas, USA. Hurricane Harvey made direct landfall over our site on 25 August 2017, uniformly decreasing soil nutrients and impacting the spatial patterns of total soil sulfide accumulation ( $\delta^{34}\text{S}$ ). To test how mangrove cover affected carbon processing and retention after the hurricane, we measured litter breakdown rates ( $k$ ) of *A. germinans* and *S. alterniflora* in surface soils and associated microbial respiration rates, and fast- and slow-decomposing standard litter substrates (green and red tea, respectively) in subsurface soils (15 cm depth). Soil temperatures were lower in mangrove than marsh cells, and *A. germinans* litter  $k$  increased linearly with plot-level mangrove cover. Breakdown rates of *S. alterniflora* and fast-decomposing green tea litter increased nonlinearly with mangrove cover (highest  $k$  at intermediate % cover). Slow-decomposing red tea had similar  $k$  in all plots and was highest where soil  $\delta^{34}\text{S}$  was greatest. Microbial respiration rates ( $R$ ) did not change with plot-level mangrove cover for either *S. alterniflora* or *A. germinans* litter. Respiration associated with *S. alterniflora* litter was highest in interior marsh cells, and  $R$  associated with *A. germinans* litter was similar between fringe and interior mangrove cells. Despite widespread declines in soil nutrient concentrations and increases in  $\delta^{34}\text{S}$ , all predicted to decrease  $R$  and  $k$ , post-hurricane carbon processing increased with

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mangrove cover in coastal wetlands. Our results indicate that disturbances can reduce local plant identity effects and may enhance carbon loss.

#### KEYWORDS

*Avicennia germinans*, biogeochemistry, disturbance, nutrients, *Spartina alterniflora*, sulfide

## INTRODUCTION

Global environmental changes are altering the distribution and composition of plant species worldwide (Chen et al., 2011; Guo et al., 2017; Kominoski et al., 2013). Human activities in coastal ecosystems are causing declines in mangroves in some regions (Davidson et al., 2018), while in other places, mangroves are expanding poleward (Cavanaugh et al., 2014; Kelleway et al., 2017). Increased minimum temperature drives mangrove expansion, at many sites, because freeze events cause dieback and reduction in mangrove cover (Cavanaugh et al., 2014; Perry & Mendelsohn, 2009). Expansion and contraction of mangroves in North America is occurring with changes in the frequency and intensity of extreme cold events at subtropical latitudes (Osland et al., 2017; Saintilan et al., 2014). In coastal Texas, salt marsh and mangrove cover have alternated over the past 100 years as mangroves have gradually expanded during warm periods and abruptly contracted during severe freezes (Armitage et al., 2015; Osland et al., 2017). Widespread expansion of mangroves throughout the entire Gulf Coast of the United States is expected in the future due to reduced frequency and severity of severe freeze events (Gabler et al., 2017; Osland et al., 2013), with largely unknown effects on the ecosystem-scale processes and services provided by coastal wetlands (Guo et al., 2017; Kelleway et al., 2017; Perry & Mendelsohn, 2009).

Mangroves increase sediment retention and accretion, reduce erosion, and increase carbon and nutrient storage (Breithaupt et al., 2012; Charles et al., 2020; Kelleway et al., 2017; Pennings et al., 2021). Aboveground, mangroves can decrease organic matter processing through inputs of relatively recalcitrant allochthonous litter (Charles et al., 2020; Rovai et al., 2018) and by reducing air and surface soil temperatures compared to marshes (Charles et al., 2020; Guo et al., 2017). Belowground, mangroves contribute higher root biomass per unit area than marshes (Charles et al., 2020). However, mangroves can also entrain labile marine subsidies that may enhance surficial breakdown of labile and recalcitrant organic matter, and mangrove roots may stimulate the subsurface breakdown of organic matter by oxygenating soils (Charles et al., 2020). At the landscape level,

increases in mangrove cover can attenuate marine allochthonous subsidies, such as wrack (Charles et al., 2020; Doughty et al., 2017). Therefore, as mangrove cover increases in transitional wetlands, it is expected that organic matter processing will also likely increase (Charles et al., 2020).

Hurricanes transform vegetation and soil composition in coastal ecosystems and can both increase and decrease nutrient availability (Castañeda-Moya et al., 2010, 2020; Kuhn et al., 2021). However, it is uncertain how hurricane-induced changes in soil chemistry interact with changes in marsh–mangrove composition to affect soil organic matter processes that are fundamentally linked to carbon storage. We conducted a large-scale experimental vegetation manipulation in Coastal Texas, USA, in transitional marsh–mangrove ecotone holding geomorphic setting and other factors constant (Guo et al., 2017; McKee & Vervaeke, 2017). We tested how mangrove–marsh identity and cover (composition) in coastal wetlands affected surface and subsurface soil litter breakdown rates and associated microbial respiration after Hurricane Harvey, which made landfall on coastal Texas on 25 August 2017. We tested for species identity (marsh vs. mangrove) and cell location (fringe vs. interior) effects on labile and recalcitrant litter breakdown and microbial respiration rates along a gradient in plot-level mangrove cover. In our prior research, we measured higher rates of black mangrove (*Avicennia germinans*) litter breakdown in mangrove than marsh cells and these rates increased with increasing plot-level mangrove cover (Table 1; Charles et al., 2020). However, we also reported declines in nutrient (nitrogen and phosphorus) concentrations and increases in total sulfide accumulation as indicated by  $\delta^{34}\text{S}$  in accreted surface sediments and soils in both marsh and mangrove cells, especially in plot fringes, following Hurricane Harvey (Table 1; Kuhn et al., 2021). As post-hurricane soil nutrient concentrations uniformly decreased in marsh and mangrove cells (Kuhn et al., 2021), we predicted litter breakdown rates would be lower than pre-hurricane (Charles et al., 2020). As total soil sulfide accumulation was highest in fringe cells post-hurricane (Kuhn et al., 2021), we predicted lower litter breakdown and microbial respiration rates in fringe than interior cells (both marsh and mangrove). We expected labile litter to be less sensitive than recalcitrant

**TABLE 1** Summary of major biogeochemical trends in soil (percent [%] carbon [C], nitrogen [N], phosphorus [P], and total sulfide accumulation as indicated by isotopic sulfur [ $\delta^{34}\text{S}$ ]) and litter breakdown rates ( $k$ ) before and after Hurricane Harvey (25 August 2017) made direct landfall over coastal wetlands in Port Aransas, Texas

Soil chemistry and litter breakdown rates											
	%C		%N		%P		$\delta^{34}\text{S}$ (‰)		$k$		
Characteristic	Before	After	Before	After	Before	After	Before	After	Before	After labile	After recalcitrant
Type	$m < M$	NS	$m < M$	NS	$m < M$	NS	NS	NS	$m < M$	$m > M$	NS
Location	$f > i$	NS	$f > i$	NS	$f > i$	NS	$f > i$	$f < i$	$f < i$	NS	NS
Cover	low < high	NS	low < high	NS	NS	NS	NS	NS	low < high	low > high	low < high

Note: Type refers to marsh ( $m$ ) or mangrove ( $M$ ) dominant vegetation type within  $3 \times 3$ -m cells. Location refers to fringe ( $f$ ) and interior ( $i$ ) cells within  $24 \times 42$ -m coastal plots. Cover refers to the plot-level mangrove cover (0%–100%) gradient from low (<50%) to high (>50%). Nonsignificant (NS) differences in categorical comparisons are noted. Trends are derived from actual data analyses in Charles et al. (2020) and Kuhn et al. (2021).

litter to mangrove cover and post-hurricane changes in soil chemistry.

## METHODS

### Study site and experimental design

Our study was conducted on Harbor Island, near Port Aransas, Texas (27.86°N, 97.08°W), in the Mission-Aransas National Estuarine Research Reserve. The vegetation at the site was initially dominated (90%–100% cover) by *A. germinans* with small patches (~10% cover) of salt marsh vegetation (mostly the succulents *Batis maritima* and *Sarcocornia* spp. and the grass *Spartina alterniflora*). In 2012, we established 10 experimental plots ( $42 \times 24$  m) along the edge of the Lydia Ann Channel. We removed mangroves from the plots by cutting them at the soil surface to create a gradient of mangrove cover (nominally 0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100% mangrove cover). The plots were arranged in three blocks, with each block containing at least one low mangrove cover, one intermediate mangrove cover, and one high mangrove cover plot (Appendix S1: Figure S1; Guo et al., 2017). To facilitate maintenance and to simulate the natural patchiness of the vegetation, mangroves were removed or left in place within  $3 \times 3$ -m cells in a stratified random checkerboard pattern. Marsh vegetation naturally recolonized most cleared cells within 2 years (Guo et al., 2017). In each plot, we selected four  $3 \times 3$ -m cells along the coastal fringe (fringe cells in the front third of each plot) and four  $3 \times 3$ -m cells within the plot interior (interior cells). Replicate cells ( $n = 8$  per plot) were all marsh (in the 0% mangrove plot), all mangrove (in the 100% mangrove plot), or half marsh and half mangrove (in mixed-species plots) for a total of  $n = 80$  replicates.

On 25 August 2017, experimental plots were directly affected by Hurricane Harvey, a Category 4 storm that made landfall nearby (Appendix S1: Figure S1). Plots were exposed to hurricane force winds exceeding 119 km/h for approximately 6 h, with gusts up to 225 km/h (NOAA, 2019). A tide gauge at Port Aransas, near the experimental plots, recorded a storm surge of 1.6 m above mean lower low water (MLLW) (NOAA, 2019), and estimates of storm surge based on debris deposition and other flood evidence indicated a storm surge of up to 2.4 m (USGS, 2019). Storm surge flooding (0.8 m above MLLW) persisted for approximately 6 h.

### Soil temperature

Throughout the experiment, we recorded soil temperature continuously (30-min intervals) using HOBO temperature sensors (Onset Computer Corporation, Bourne, Massachusetts, USA) placed at 5 cm depth. Temperature sensors were inserted into interior cells of the 0% mangrove (100% marsh) and 100% mangrove plots ( $n = 2$  total).

### Subsurface total soil sulfide accumulation

We previously reported that soil nutrient concentrations decreased post-hurricane and were similar in marsh and mangrove cells and along plot-scale mangrove cover (Kuhn et al., 2021; see Table 1). Here, we focus on total soil sulfide accumulation as indicated by  $\delta^{34}\text{S}$ , which changed over time post-hurricane and varied among wetland types and locations (Kuhn et al., 2021). In 2017 and 2018, we collected soil cores (5 cm diameter  $\times$  30 cm depth) in each of the same randomized cells ( $n = 8$  per

plot) to measure chemistry in subsurface soils. We removed roots from cores and homogenized soils prior to chemical analysis. Subsamples were dried at 60°C to a constant dry mass. We ground and homogenized portions with an 8000-D ball mill (Spex SamplePrep, Metuchen, New Jersey, USA). We measured stable isotopes of sulfur from subsurface soils (0–30 cm). The ratios of heavy to light stable isotopes are expressed as  $\delta$  to indicate relative depletion (–) or the enrichment (+) of the heavy isotope compared to the lighter isotope relative to a standard, according to the formula:  $\delta X (\text{‰}) = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 10^3$  where  $X$  is  $^{34}\text{S}$  and  $R$  is  $^{34}\text{S}:^{32}\text{S}$ . Results were presented as deviations from a standard (Canyon Diablo troilites for S). Repeatability was  $\delta^{34}\text{S} \pm 0.3\text{‰}$ .

## Surface and subsurface organic matter breakdown rates

On 23 June 2017, we deployed rooibos (red) and green tea standard substrate litter at 15 cm depth of soil in marsh and mangrove cells at the front (fringe) and back (interior) of each of the 10 plots (see Keuskamp et al., 2013). Tea litterbags were retrieved on 15 June 2018 after 357 days of incubation. We calculated green and red tea breakdown rates ( $k$ ) using the exponential decay equation  $M_t = M_0 \times e^{-kt}$ , whereby  $M_t$  is the final dry mass,  $M_0$  is the initial dry mass, and  $t$  is time in days ( $k$ , per day). Due to disturbances from hurricane in August 2017, we were unable to recover red tea litter from the 0% mangrove cover plot.

We harvested *S. alterniflora* and *A. germinans* green leaves (hereafter litter) from the field on 7 November 2018 and allowed them to air dry for 24 h. Approximately 5 g of litter was placed into 1-mm nylon mesh bags ( $5 \times 15$  cm). On 9 November 2018, litterbags were deployed into replicate marsh and mangrove cells in fringe and interior zones in each of the 10 plots. Replicate cells ( $n = 8$  per plot) were all marsh (in the 0% mangrove plot), all mangrove (in the 100% mangrove plot), or half marsh and half mangrove (in mixed plots) for a total of  $n = 80$  replicates. A total of  $n = 80$  litterbags were deployed. Litterbags containing *S. alterniflora* litter were deployed in marsh cells. Litterbags containing *A. germinans* litter were deployed in mangrove cells. On 24 June 2019, litter samples were retrieved after 227-day incubation and returned to the laboratory on ice. We used the exponential decay equation (above) to quantify breakdown rates per day ( $k$ , per day).

As teabags and litterbags were deployed on different dates, we calculated breakdown rates per degree-day ( $k$ , per degree-day). We found similar treatment effects for  $k$  from teabags and litterbags reported per day as per degree-day. Therefore, we only present results for  $k$  from teabags and

litterbags per day. Data for both  $k$  per day and per degree-day are published and freely available (Kominoski et al., 2021).

## Microbial respiration rates

As an indicator covariate of decomposition rates, we measured microbial respiration rates ( $R$ ) on decomposing *S. alterniflora* and *A. germinans* litter after field incubation. Subsamples of field incubated litter were placed in glass vials (40 mL) in the laboratory. Vials were completely filled with filtered site seawater to remove any gas head space, sealed with caps, and placed in the dark for 1 h. Dissolved oxygen concentrations were measured at the beginning and end of laboratory incubations using YSI ProODO dissolved oxygen meters (Yellow Springs, Ohio, USA). Additional vials ( $n = 2$ ) containing only site water served as controls. Oxygen consumption rates were determined as the slope of the regression of dissolved oxygen concentration over time minus the slope of the control, and respiration rates were expressed per gram dry mass of litter per hour.

## Data analyses

All data are publicly available online (Kominoski et al., 2021). We used analysis of variance (ANOVA) to test for differences in litter breakdown rates in fringe and interior marsh and mangrove cells. We fitted nonlinear relationships for  $k$  and  $R$  between plot-level mangrove cover (0%–100%) using the *geom\_smooth* and *stat\_poly\_eq* functions within the “ggpmisc” (Aphalo, 2021) and “gridExtra” extension (Auguie, 2017) in the “ggplot2” package in R (Wickham, 2016). We used simple linear regressions to test for effects of subsurface total soil sulfide accumulation on surface and litter  $k$  and  $R$ . All statistical analyses were performed with R version 3.6.1 and RStudio version 1.2.1335 (R Core Team, 2020).

## RESULTS

### Soil temperature

Soil temperatures were similar between the 100% marsh plot and the 100% mangrove plot. During tea litter incubations, which included summer dates, median soil temperatures were 23.4°C (range: 6.7–32.3°C) in marsh cells and 24.1°C

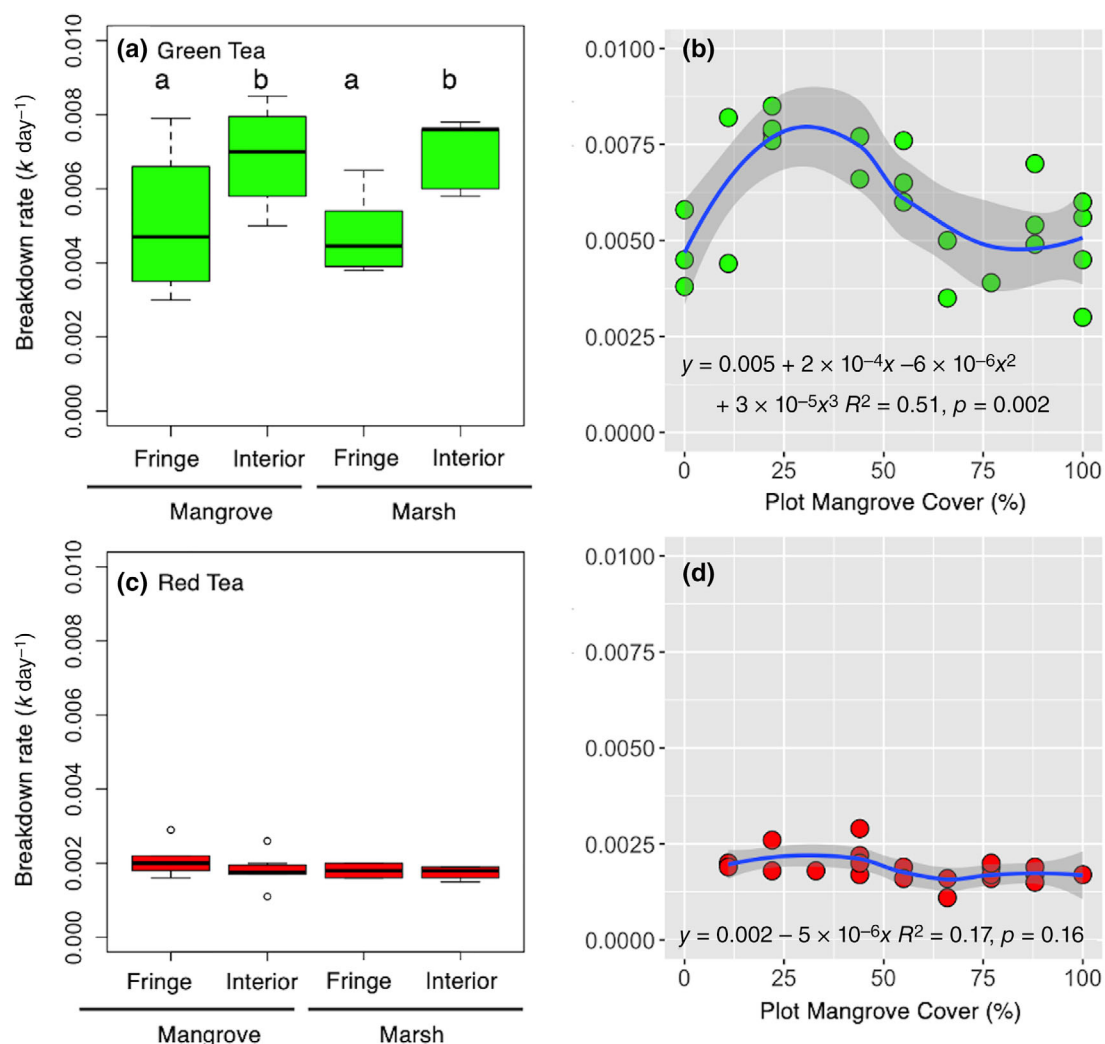
(range: 5.5–31.5°C) in mangrove cells (Appendix S1: Figure S2A,B). During plant litter incubations, which omitted the hottest summer months, median soil temperatures were 18.2°C (range: 10.6–30.2°C) in marsh cells and 18.3°C (range: 11.5–29.8°C) in mangrove cells (Appendix S1: Figure S2A,B).

### Subsurface total soil sulfide accumulation

We observed depleted  $\delta^{34}\text{S}$  values in coastal (fringe) marsh cells 1 month after the hurricane (2017), and by 1 year post-hurricane (2018),  $\delta^{34}\text{S}$  values were further depleted in both marsh and mangrove fringe soils (Table 1; Kominoski et al., 2021).

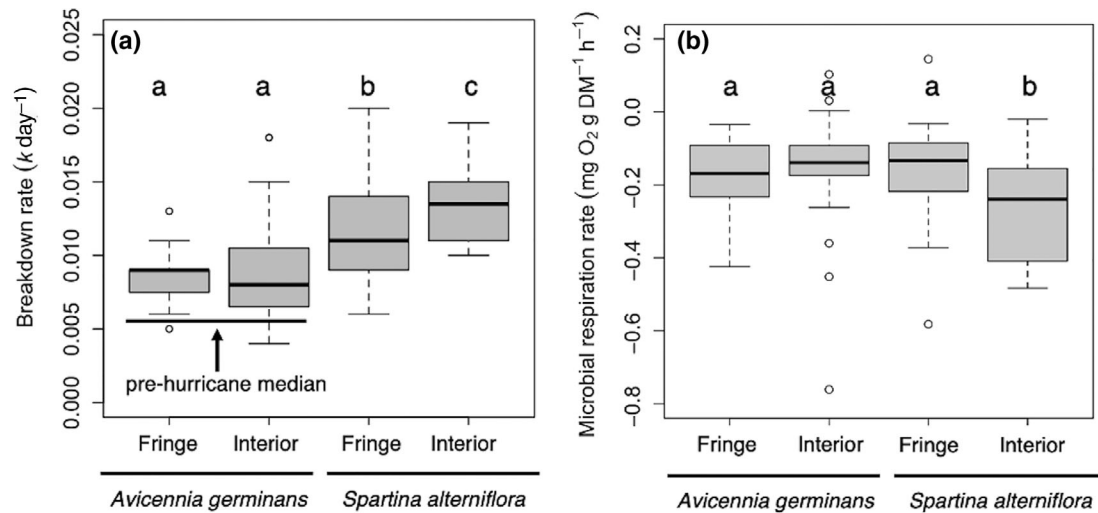
### Surface and subsurface organic matter breakdown rates

Subsurface green tea  $k$  was higher in interior compared to fringe of plots (for both marsh and mangrove cells) (Figure 1a; ANOVA:  $F_{3,20} = 4.3$ ,  $p = 0.02$ ). Green tea  $k$  was highest at intermediate plot-level mangrove cover (Figure 1b;  $R^2 = 0.51$ ,  $p < 0.01$ ). Subsurface red tea  $k$  was similar among locations and cells (Figure 1c; ANOVA:  $F_{3,18} = 0.9$ ,  $p = 0.43$ ), and red tea  $k$  was also similar along the gradient in mangrove cover (Figure 1d;  $R^2 = 0.17$ ,  $p = 0.16$ ). Surface *S. alterniflora*  $k$  was higher in interior than fringe marsh cells, whereas *A. germinans* litter  $k$  was similar in interior and fringe mangrove cells (Figure 2a; ANOVA:  $F_{1,70} = 19.5$ ,  $p < 0.001$ ). Surface *S. alterniflora*



**FIGURE 1** Post-hurricane subsurface breakdown rates for (a, b) green and (c, d) red tea litter per day ( $k$  day $^{-1}$ ) in fringe and interior marsh and mangrove cells along a gradient in plot-level mangrove percent cover. Letters denote significant differences ( $p < 0.05$ ) using analysis of variance. Trend lines, equations, and goodness of fits are associated with third-order polynomial (green tea) and simple nonlinear regressions (red tea). *Note:* Data for red tea missing from plot with 0% mangrove cover





**FIGURE 2** Post-hurricane (a) surface breakdown rates ( $k$ , per day) for *Spartina alterniflora* and *Avicennia germinans* litter, and (b) microbial respiration rates associated with *Spartina alterniflora* and *Avicennia germinans* litter in fringe and interior marsh and mangrove cells. Higher respiration rates correspond with more negative rates of change in dissolved oxygen. Pre-hurricane median  $k$  per day for *A. germinans* from Charles et al., 2020. Letters denote significant differences ( $p < 0.10$ ) using analysis of variance

litter  $k$  peaked at lower plot-level mangrove cover and declined above 33% plot-level mangrove cover but was not statistically significant (Figure 3a;  $R^2 = 0.11$ ,  $p = 0.31$ ). In contrast, surface *A. germinans* litter  $k$  increased with plot-level mangrove cover (Figure 3c;  $R^2 = 0.21$ ,  $p = 0.04$ ).

### Microbial respiration rates

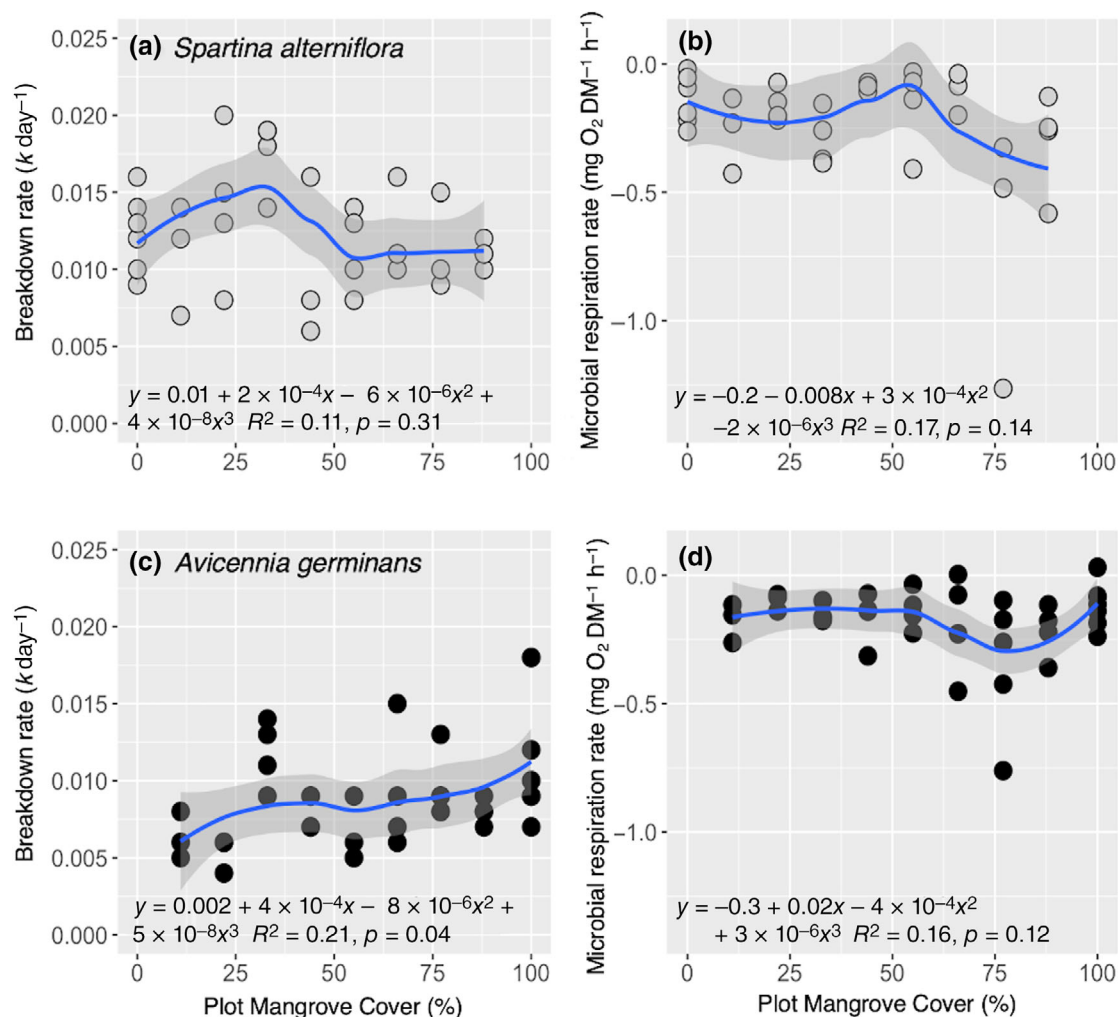
Overall, microbial  $R$  associated with surface *A. germinans* and *S. alterniflora* litter was similar (Figure 2b; ANOVA:  $F_{1,70} = 1.4$ ,  $p = 0.24$ ) and  $R$  was not affected by interior or fringe location within plots (Figure 2b; ANOVA:  $F_{1,70} = 2.0$ ,  $p = 0.16$ ). However,  $R$  on *S. alterniflora* was marginally greater in interior compared to fringe marsh cells (Figure 2b; ANOVA:  $F_{1,70} = 3.5$ ,  $p = 0.07$ ). Respiration rates did not change with plot-level mangrove cover for *S. alterniflora* (Figure 3b;  $R^2 = 0.17$ ,  $p = 0.14$ ) and *A. germinans* litter (Figure 3d;  $R^2 = 0.16$ ,  $p = 0.12$ ).

### Effects of sulfide on litter breakdown and microbial respiration rates

We measured depleted  $\delta^{34}\text{S}$  values (indicating increased total sulfide accumulation) in both marsh and mangrove cells of the fringe zones of plots. Red tea litter  $k$  was higher in soils with higher total sulfide accumulation, whereas all other litter  $k$  were unaffected (Figure 4a–d). We did not detect effects of total soil sulfide accumulation on  $R$  associated with decomposing surface litter (*S. alterniflora* and *A. germinans*) (Figure 5a,b).

## DISCUSSION

Our results indicate that the effect of marsh and mangrove vegetation on soil carbon processing changed after hurricane disturbance. Before the storm, there were strong plant identity effects on decomposition rates, regardless of litter type, with higher rates in mangrove and in marsh cells and in plots with higher mangrove cover (Table 1; Charles et al., 2020). After the hurricane, the drivers of organic matter processing shifted away from stronger plant identity effects observed pre-hurricane (Charles et al., 2020), to complex interactive effects of plant identity, cell location, and litter quality driving soil organic matter processing. Based on prior findings from our experimental sites (Charles et al., 2020), we expected faster *S. alterniflora* litter  $k$  in plots dominated by marshes (lower plot-level mangrove cover) and faster *A. germinans* litter  $k$  in plots dominated by mangroves (higher plot-level mangrove cover), and our results supported this prediction. We also predicted lower *A. germinans* litter  $k$  compared to pre-hurricane (Charles et al., 2020), as soil nutrients decreased and total soil sulfide accumulation increased post-hurricane (Kuhn et al., 2021). Our results were contrary to this hypothesis, as we measured higher *A. germinans*  $k$  post-hurricane compared to pre-hurricane (Charles et al., 2020). We measured higher loss rates of labile organic matter (green tea, *S. alterniflora* litter) in interior marsh cells and in plots with lower mangrove cover, and higher loss rates of recalcitrant organic matter (red tea, *A. germinans* litter) in soils with higher total soil sulfide accumulation and in plots with higher mangrove cover. Surface and

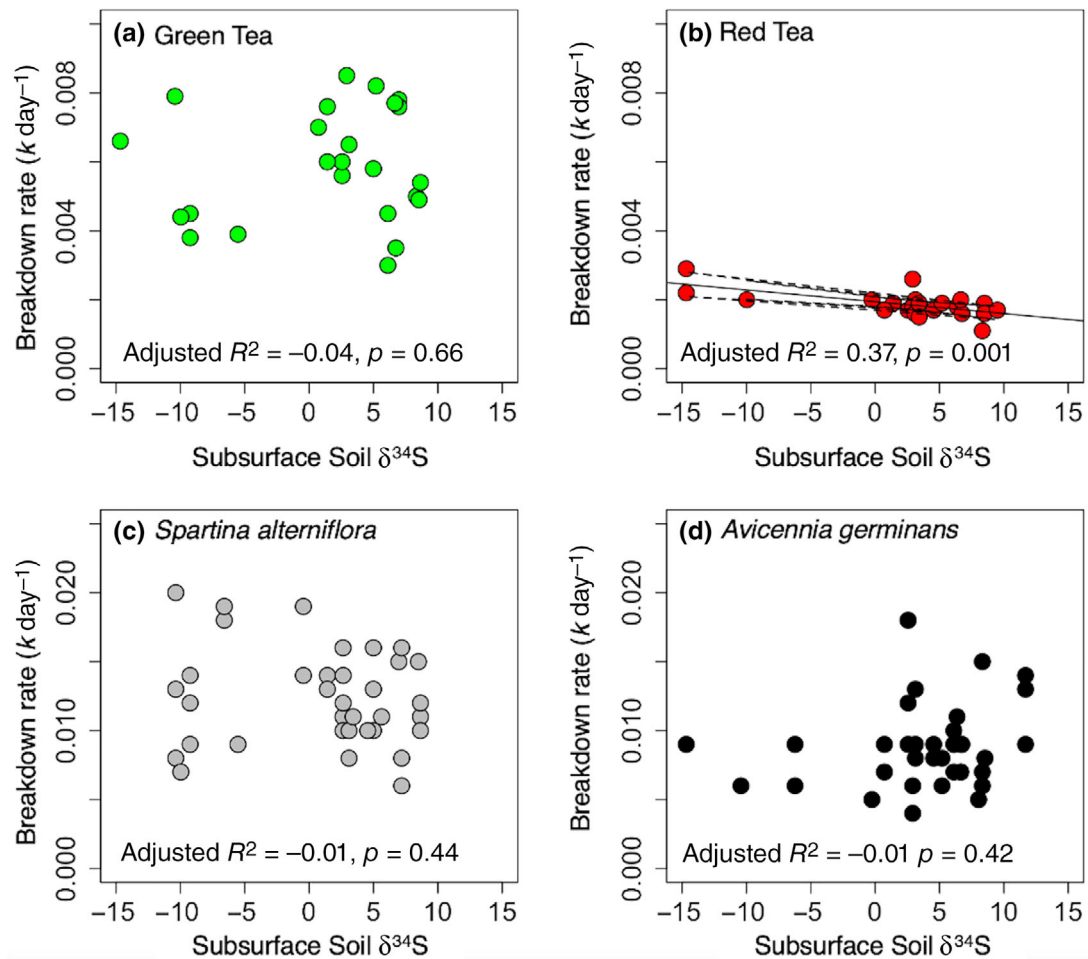


**FIGURE 3** Post-hurricane (a, c) surface breakdown rates ( $k$ , per day) of *Spartina alterniflora* and *Avicennia germinans* litter, (b, d) microbial respiration rates associated with *Spartina alterniflora* and *Avicennia germinans* litter in marsh and mangrove cells along a gradient in plot-level mangrove percent cover. Higher respiration rates correspond with more negative rates of change in dissolved oxygen. Trend lines, equations, and goodness of fits are third-order polynomials of nonlinear regressions

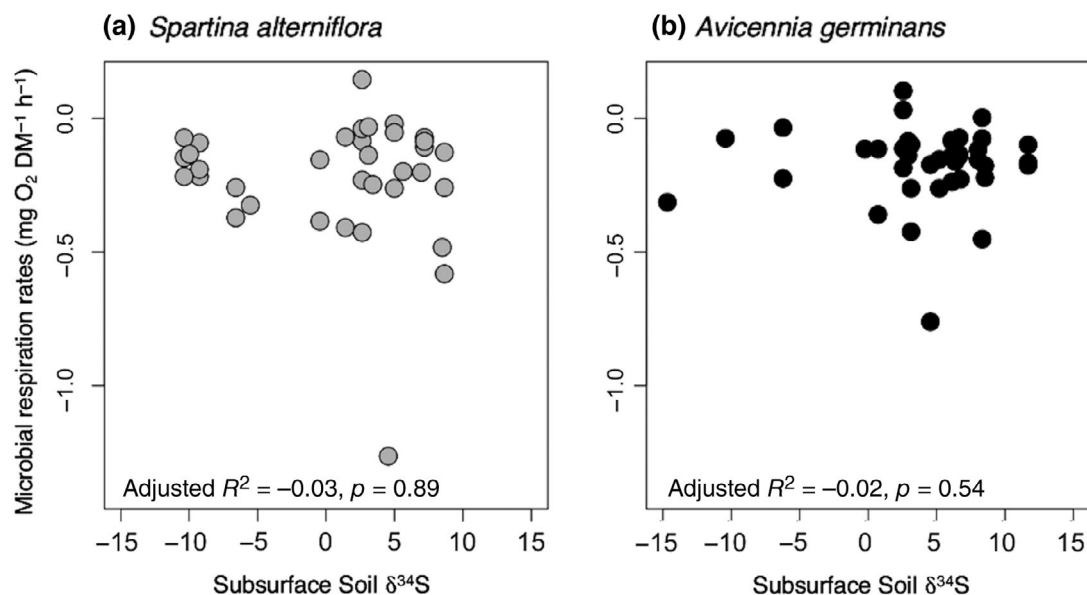
subsurface litter  $k$  and  $R$  were not inhibited by sulfide accumulation, as we had predicted. Overall, labile organic matter broke down faster in marsh-dominated wetlands, and recalcitrant litter broke down faster in mangrove-dominated wetlands post-hurricane.

Different mechanisms likely explain patterns and trends of labile and recalcitrant organic matter processing in ecosystems. Breakdown rates of labile organic matter may be higher in wetlands with more marshes than mangroves due to higher irradiation and temperature in the less dense marsh canopies, although we measured similar median subsurface soil temperatures in marsh and mangrove cells (see “Results” and Appendix S1: Figure S2). Our previous studies detected a hump-shaped relationship between soil surface temperatures and plot-level mangrove cover, whereby the highest temperatures were

measured at 44%–55% mangrove cover (Charles et al., 2020; Guo et al., 2017). In our current study, green tea and *S. alterniflora* litter breakdown rates had similar hump-shaped trends with plot-level mangrove cover, suggesting temperature was an important driver of labile organic matter breakdown. In addition, physical abrasion from eroding and depositing sediment, which was higher in plots with lower mangrove cover (Pennings et al., 2021), may contribute to higher loss rates in soil surfaces for faster-decomposing, labile organic matter. In our experimental plots, edge erosion following the storm was >5 m where mangroves were absent (100% marsh cover) and was <0.5 m in plots with mangroves present (11%–100% mangrove cover) (Armitage et al., 2019). Post-hurricane accreted soil depth was more than two times higher in marsh cells than in mangrove cells (Armitage



**FIGURE 4** Post-hurricane litter breakdown rates ( $k$ , per day) for subsurface (a) green tea and (b) red tea, and surface (c) *Spartina alterniflora* and (d) *Avicennia germinans* along a gradient in subsurface total soil sulfide accumulation as indicated by  $\delta^{34}\text{S}$ . Goodness of fit determined from linear regressions



**FIGURE 5** Post-hurricane litter breakdown microbial respiration rates associated with (a) *Spartina alterniflora* and (b) *Avicennia germinans* surface litter along a gradient in subsurface total soil sulfide accumulation as indicated by  $\delta^{34}\text{S}$ . Goodness of fit determined from linear regressions



et al., 2019). These conditions likely favored higher breakdown rates of labile organic matter (*S. alterniflora* and green tea litter), but we did not observe this pattern for recalcitrant litter (*A. germinans*). In contrast, higher breakdown rates of *A. germinans* in mangrove-dominated plots suggest a possible “home field” advantage of meta-zoan and microbial communities adapted to and preferentially consuming recalcitrant organic matter, which has been observed in other wetland and aquatic ecosystems (Kominoski et al., 2012; Smith et al., 2019; Yeung et al., 2019). Smith et al. (2019) found *A. germinans* litter *k* was two to four times higher than that of *S. alterniflora* litter irrespective of cell vegetation type (marsh, mangrove, and mixed-species), and it was suggested that this was because *A. germinans* has a lower molar C:N ratio than *S. alterniflora*. However, C:N of *A. germinans* litter from our sites was higher (66–72) (Charles et al., 2020) than that has been reported elsewhere (47–55) (Lawton-Thomas, 1997; Twilley et al., 1986), making it more similar in nutrient content to *Spartina detritus* (65–92) (Breteler et al., 1981; White & Howes, 1994), and making this an unlikely mechanism in our study.

Storm-induced changes in soil chemistry and redox conditions explained some, but not all, post-hurricane patterns of organic matter processing. *Avicennia germinans* litter *k* was slightly lower pre-hurricane (Charles et al., 2020) than post-hurricane (this study) and increased with plot-level mangrove cover during both time periods. Our previous research found a decline in surface and subsurface soil nutrient (nitrogen and phosphorus) concentrations and up to a five times increase in total soil sulfide accumulation as indicated by  $\delta^{34}\text{S}$  post-hurricane (Kuhn et al., 2021). Sulfide accumulation increased in soils of both marsh and mangrove cells in marsh-dominated wetland ( $\leq 44\%$  plot-level mangrove cover). Although sulfide accumulation can reduce rates of organic matter breakdown and soil biogeochemical cycling (Chambers et al., 2013; Joye & Hollibaugh, 1995; Mendelsohn et al., 1999), we only observed sulfide effects on red tea litter *k* (and rates were surprisingly higher in soils with greater total sulfide accumulation). It is possible that we did not detect greater effects of sulfide in our microtidal wetlands due to noncontinuous flooding. The extensive flooding event that occurred during and after Hurricane Harvey and following the hurricane undoubtedly increased total soil sulfide accumulation in our plots, especially where subsequent erosion and deeper water occurred in the fringe zone of plots with lower mangrove cover (Pennings et al., 2021). Higher rates of red tea *k* and total sulfide accumulation in this study generally occurred in fringe cells of plots where erosion was higher (Pennings et al., 2021), but why we did not detect similar patterns for green tea,

*A. germinans*, and *S. alterniflora* litter *k* and sulfide accumulation is unclear.

The effects of mangrove cover on post-hurricane carbon processing were nonlinear. Our experimental findings show similar nonlinear effects of mangrove cover on shoreline erosion (Armitage et al., 2019; Pennings et al., 2021). Mangroves provided greater shoreline protection services than marshes (Armitage et al., 2019; Doughty et al., 2017). Mangrove vegetation was more impacted aboveground by the hurricane than marsh vegetation (Armitage et al., 2019), but belowground reductions in root biomass post-hurricane were measured throughout all plots and in marsh and mangrove cells (Kuhn et al., 2021). Prior to the hurricane, root biomass was 61% greater in mangrove than marsh cells (Charles et al., 2020) but declined by up to 80% in all cells post-hurricane (Kuhn et al., 2021). Although many aboveground physical attributes of coastal wetlands (e.g., microclimate, erosion, and deposition) appear to shift around a 50% mangrove cover threshold (Guo et al., 2017; Pennings et al., 2021), post-hurricane changes in belowground processes appear to be more homogeneous and develop over time. For example, although marshes were immediately impacted by erosion and total sulfide accumulation, patterns of both stressors continued to converge in marshes and mangroves more than a year post-hurricane (especially in fringe cells; Kuhn et al., 2021). Collectively, these stressors can lead to legacies of reduced root biomass and delayed mortality in wetlands post-hurricane (Kuhn et al., 2021; Radabaugh et al., 2019). The hurricane likely disrupted the cell-scale plant identity effects on litter breakdown that we observed pre-hurricane (Charles et al., 2020) and enhanced the plot-scale mangrove cover effects we observed in post-hurricane (i.e., higher breakdown rates of labile green tea litter in marsh-dominated wetlands and higher breakdown rates of recalcitrant *A. germinans* litter in mangrove-dominated wetlands).

How disturbances interact with coastal vegetation changes to influence ecosystem services remains an uncertainty and a challenge for ecology. We discovered that differences in marsh and mangrove cover in transitional wetlands led to differences in surface and subsurface soil carbon processing in response to a major hurricane, and that pre-hurricane plant identity effects decreased while plot location effects in coastal wetland ecosystems increased. Higher carbon processing rates with increasing mangrove cover following a hurricane suggest that disturbance legacies vary among ecosystem types. Legacy effects of disturbances will depend on the impact and recovery following the event, as well as the mechanisms of the disturbance driver and the differential capacity of different ecosystems to respond (Gaiser

et al., 2020). How disturbances interact with other disturbances and environmental changes in ecosystems will determine the long-term functioning and adaptive capacity of ecosystems (Gaiser et al., 2020; Kominoski et al., 2018; Kominoski et al., 2020).

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## CONFLICT OF INTEREST


The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT


Data and novel code (Kominoski et al., 2021) are available from the Environmental Data Initiative Data Portal: <https://doi.org/10.6073/pasta/676ca962d375e90b1d06089c0cac88ba>.

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