Coastal riverine wetland biogeochemistry follows soil organic matter distribution along a marsh-to-mangrove gradient (Florida, USA)

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HIGHLIGHTS

• Three Florida Gulf coast riverine marsh-mangrove ecotones were studied.
• Vegetation ecotones were not a proxy for biogeochemical ecotones.
• Soil biogeochemical patterns differed from river to river across the landscape.
• Organic matter was the most informative metric of soil biogeochemical patterns.
• Inorganic nutrient concentrations were strongly seasonal.

GRAPHICAL ABSTRACT

Little Manatee River Peace River Fakahatchee River
Marsh Transition Mangrove Marsh Transition Mangrove Marsh Transition Mangrove

Average soil organic matter content
Max. observed surface water salinity
Average potential CO₂ production
Average potential CH₄ production

ABSTRACT

Many subtropical coastal wetland vegetation communities are transitioning from herbaceous marsh to woody mangrove, often facilitated by sea-level rise. This study investigated the relationships between vegetation community (upstream marsh, ecotone/transition, and downstream mangrove), salinity (S), and soil biogeochemistry in wetlands along three rivers on the Florida Gulf coast (the Little Manatee, Peace, and Fakahatchee Rivers). Vegetation was surveyed, and soil and water samples were collected during both the dry and the wet season and analyzed for biogeochemical properties (soil: bulk density, pH, organic matter, extractable inorganic and total nutrients, dissolved organic carbon (DOC), and microbial biomass carbon; water: inorganic nutrients and DOC) and processes (greenhouse gas production) while salinity and water level were continuously monitored in the field. Results indicated landscape-scale patterns in soil biogeochemistry differed significantly by river and were most strongly correlated with soil organic matter content, regardless of vegetation community or salinity regime. Contrary to expectations, soil organic matter content gradients were not always inversely related to salinity gradients, and methane production was observed in moderate- (S = 12) and high- (S = 34) salinity mangrove communities. The vegetation ecotone experienced seasonally variable salinity and did not serve as a true biogeochemical intermediate between the marsh and mangrove communities. This study demonstrates the need for site-specific studies of biogeochemical gradients in coastal wetlands and indicates the marsh-to-mangrove ecotone is not a proxy for salinity or biogeochemical tipping points. Instead, soil organic matter content is suggested as the most relevant indicator of biogeochemical properties and processes in wetlands along coastal rivers, superseding vegetation community or salinity.

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1. Introduction

Coastal wetland ecosystems range from salt marshes in temperate climates to mangrove forests in the tropics and provide a host of ecosystem services, including storm surge buffering, nutrient removal, water storage, wildlife habitat, and carbon storage (Barbier et al., 2011; Costanza et al., 1998; Sun et al., 2018). In the sub tropics, many marshes are transitioning into mangrove-dominated ecosystems (Coldren et al., 2019; Eslami-Andargoli et al., 2009; Giril and Long, 2016; Kelleway et al., 2016; Liu et al., 2017). While the frequency of intense freeze-events dictates latitudinal mangrove expansions (Cavanaugh et al., 2014), sea-level rise and decreased freshwater flow are important drivers of landward mangrove transgression in areas where the areal extent is not limited by temperature (Krauss et al., 2011). An increase in salinity can give mangroves a competitive advantage over less salt-tolerant brackish and freshwater marsh vegetation (Spalding and Hester, 2007), and, as long as propagules are present, mangroves can fill the void left by dead and dying glyophytes (Herbert et al., 2015). This shift from herbaceous to woody vegetation changes both aboveground ecophysiology and belowground biogeochemistry. For example, mangroves are taller and store more carbon aboveground than marshes (Kelleway et al., 2016), and young mangroves in Florida can cycle nutrients more rapidly than neighboring salt marsh (Steinmuller et al., 2020). Roots of Avicennia germinans in a mesohaline system can grow nearly half a meter into the soil (Purvaja et al., 2004), possibly stimulating local microbial activity in previously anoxic wetlands (Ball, 1988).

As mangroves gradually transgress landward within coastal wetland landscapes, their encroachment co-occurs with the existing gradients of topography, salinity, and tidal inundation. Generally, soil organic matter (OM) content and nutrient concentrations (carbon (C), nitrogen (N), and phosphorous (P)) are highest near the freshwater end of the coastal salinity gradient, decreasing downstream to the saltwater end-member community (Craft, 2007; Loomis and Craft, 2010; Morrissey et al., 2014; Odum, 1988; Twilley and Chen, 1999; Wieski et al., 2010; Williams et al., 2014). Salinity alone can alter biogeochemical processes in these nutrient-rich freshwater tidal wetlands, which in turn, affects the rates in which carbon dioxide (CO2) and methane (CH4) are emitted from soil as end-products of microbial mineralization. Vegetation can become stressed by the heightened salinity and therefore reduce root growth (Conner et al., 1997; Wilson et al., 2018), which further alters substrate availability for microbial respiration and could lead to a decrease in CO2 production (Neubauer et al., 2013). In other wetland soils, saltwater intrusion increases soil respiration and nutrient flux into the water column. For example, laboratory incubations of freshwater soils with low (S = 0.5), moderate (S = 14), and high (S = 35) salinity seawater increased CO2 production for two weeks after the onset of saline conditions (Chambers et al., 2011). In a flow-through reactor, freshwater soils exposed to artificial seawater (S = 10) released bound PO43− and NH4+ (Winston et al., 2006). However, this stimulation effect may be short-term, as overall CO2 flux decreased by 83% in surface soils (0–3 cm) after 3.5 years when porewater salinity increased from 0.5 to 2–5 (Neubauer et al., 2013).

Saltwater intrusion can also shift dominant pathways of microbial respiration in soils as the abundant sulfate in saline wetlands allows sulfate-reducing prokaryotes to outcompete methanogens in highly reduced soils (Capone and Kiene, 1988). Methanogenesis usually decreases dramatically when freshwater soils are introduced to low-salinity water (Chambers et al., 2011, 2013; Edmonds et al., 2009; Helton et al., 2014; Livesley and Andrusiak, 2012; Neubauer, 2013; Weston et al., 2006). Salinity as low as one has been found to suppress methanogenesis in favor of sulfate reduction in the Cape Fear estuary in North Carolina, USA (Hackney and Avery, 2015), while S = 10 was identified as the threshold between CH4 and CO2 dominance in tidal freshwater marsh soils in China (Wang et al., 2017). However, others have demonstrated methane production can be sustained into low and moderate salinity ranges (Bartlett et al., 1987; Wang et al., 2017; Weston et al., 2011) and sometimes reaches a local maximum at oligo- or mesohaline wetlands (Weston et al., 2014; Poffenbarger et al., 2011).

Due to the co-occurrence of mangrove encroachment and the salinity gradients known to influence biogeochemistry, we sought to investigate the utility of highly visible shifts in vegetation communities in serving as a proxy for local saltwater intrusion and accompanying changes in biogeochemical properties and processes. For example, does the landward extent of mangroves reflect a tipping point in the salinity regime, and can anything be deduced about C, N, and P cycling patterns simply based on observed vegetation transitions? Specifically, the objectives of this study were to 1) investigate physicochemical gradients and soil biogeochemical properties and processes along three coastal riverine wetland vegetation gradients from marsh to mangrove communities and 2) determine if the biogeochemical gradients observed across the ecotone are consistent across the landscape (i.e., among the three study rivers). In other words, are readily observable vegetation communities a robust indicator of other physical, chemical, and biological properties in coastal wetlands? An observational field study was conducted in the coastal wetlands along three subtropical tidal rivers on Florida’s Gulf coast using a three-site transect that spanned the marsh-mangrove ecotone to meet these objectives. Soil and water samples were collected in both the dry and the wet seasons to account for the effects of changing abiotic conditions. We expected the upstream marsh would have the highest concentrations of nutrients, soil OM, and CH4 production, all of which would progressively decrease as one moves downstream into the transition and mangrove communities. We further expected spatial patterns in biogeochemical properties from marsh to mangrove would remain consistent across the landscape, regardless of river, and be primarily driven by salinity, as reflected by the dominant vegetation community.

2. Methods

2.1. River descriptions

This study was conducted along the west coast of central and south Florida, each characterized by a humid subtropical or tropical climate. The region has a dry season from November to April and a wet season from May to October. Study transects were established on the Little Manatee River (near Ruskin, FL), the Peace River (near Arcadia, FL), and the Fakahatchee River (south of Naples, FL). Three sampling locations (referred to as sites) were established along each river based on the dominant vegetation community: marsh (upstream), transition (midway with mixed vegetation), and mangrove (downstream) (Fig. 1). Site location, establishment and sampling dates, and soil series information for all rivers are in Supplementary Table 1. Fakahatchee River, in the southwest portion of the Greater Everglades, was uniquely characterized by a large, sheet-flow-dominated wetland mosaic with few shallow channels, rather than the comparatively deep and well-defined channels seen at the Little Manatee and Peace Rivers. These attributes limited access and the ability to choose sites along a defined river transect in the Fakahatchee basin. Therefore, marsh, transition, and mangrove sites were chosen based on observable differences in the dominant vegetation community within the mosaic (Fig. 1). Vegetation cover and biomass were assessed in 10 × 10 m plots between July and October 2018, using a modification of methods outlined in Radabaugh et al. (2018) to confirm that each site accurately represented the desired vegetation community. HOBO data loggers (models U24-002-C and U20-04; OnSet Computer Corporation, Bourne, MA, USA) housed in a single 1.2-m-long, 6-cm-wide PVC piezometer with 0.2-mm-wide slits along the length (22 slits per 10 cm) monitored conductivity and water level every 30 min. Piezometers were installed at each site within the intertidal zone by hammering the PVC into the soil until resistance.

Loggers were pushed to the bottom of the piezometers to ensure submergence for as much of the study period as possible. Sites were sampled during both the dry and the wet seasons (March–April and October 2018), at which point logger data were also downloaded and malfunctioning equipment identified and replaced. Salinity is reported in practical salinity units (psu), which is a unitless measurement of salinity and practically interchangeable with parts per thousand (ppt) (Reid, 2011).

2.2. Sampling design

During each sampling event, three soil cores extending to a depth of 30 cm were taken in the intertidal zone at each site within 1 m in the upstream (dry season sampling) or downstream (wet season sampling) direction of the piezometer using the push core method. Specific sampling locations within this area were chosen haphazardly to avoid coring directly on live stems. Core tubes were made of 7-cm-diameter
poly carbonate with a beveled edge. A rubber mallet and wooden board were used to pound the tube into the soil with limited soil compaction. Each core was extruded and sectioned in the field into four segments: 0–5 cm, 5–10 cm, 10–20 cm, and 20–30 cm. The 5-cm increment at the top of the core was chosen to account for what has been shown to be the most biologically active layer in wetland soils (Koretsky et al., 2005; Kostka et al., 2002) All analyses described below were performed on all depth segments. Samples were stored in polyethylene bags on ice for transport to the laboratory and kept at 4 °C until analysis. Surface water samples were also collected at each site during soil collection. Surface water samples were filtered through 0.45-μm Whatman® 42 filters (Cytiva Life Sciences, Marlborough, MA, USA) using a vacuum pump, and diluted to 50 mL to account for evaporative volume loss. Total P was determined colorimetrically on a SEAL AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI). Published detection limits for these methods were 0.003 mg L⁻¹, 0.002 mg L⁻¹, and 0.004 mg L⁻¹ for NO₃⁻, NH₄⁺, and PO₄³⁻, respectively. Detailed analytical procedures for all laboratory methods are available in Supplementary Table 3. The surface water salinity was determined in the field using a YSI ProDSS (YSI/XYlem Inc., Yellow Springs, OH, USA), and all values are reported on the practical salinity scale (Lewis, 1980).

2.3. Soil and water properties

A subsample of homogenized soil for each depth segment was dried at 70 °C in a gravity oven for three days, or until sample weight stabilized, to obtain dry bulk density (DBD) and moisture content. Any rhizomes were removed before drying, but other root material was retained. Dried soil was ground with ceramic balls in a SPEX 8000 M Mixer/Mill (SPEX Sample Prep, Metuchen, NJ, USA) for 2 min. The proportion of soil OM was calculated as the proportion of weight lost by a dried ground subsample following ashing in a muffle furnace at 550 °C for 3 h (Craft et al., 1991). Total P was measured on the ashed sample dried ground subsample following ashing in a muffle furnace at 550 °C until nutrient and dissolved organic carbon (DOC) analysis within 28 days. Surface water nutrients NO₃-, NH₄⁺, and PO₄³⁻ were quantified on a SEAL AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI). Published detection limits for these methods were 0.01, 0.05, and 0.005 mg L⁻¹, for NO₃⁻, NH₄⁺, and PO₄³⁻, respectively. Shimadzu TOC-L Analyzer (Shimadzu Scientific Instruments, Kyoto, Japan) results from non-fumigated samples were used to determine extractable DOC concentrations. The published detection limit for this method is 50 μg TC L⁻¹.

2.4. Extractable inorganic nutrients and dissolved organic C

Extractable inorganic nutrients NO₃⁻ (EPA-129-A Rev. 9), NH₄⁺ (EPA-129-A Rev. 8), and PO₄³⁻ (EPA-145-A Rev. 1; US EPA 1993) from non-fumigated samples from microbial biomass C analysis were analyzed colorimetrically on a SEAL AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI). Published detection limits for these methods were 0.01, 0.05, and 0.005 mg L⁻¹, for NO₃⁻, NH₄⁺, and PO₄³⁻, respectively. Shimadzu TOC-L Analyzer (Shimadzu Scientific Instruments, Kyoto, Japan) results from non-fumigated samples were used to determine extractable DOC concentrations. The published detection limit for this method is 50 μg TC L⁻¹.

2.5. Microbial biomass C

Microbial biomass C was measured with the chloroform fumigation method described in Vance et al. (1987) with modifications (Steinmuller et al., 2020). Duplicate soil samples of 5 g were weighed together upon return to the laboratory: one to be fumigated and one as a non-fumigated control. Non-fumigated samples were extracted with 25 mL 2 M KCl and incubated in an orbital shaker for 1 h at 25 °C and 150 rpm. centrifuged for 10 min at 5000 rpm and filtered through 0.45-μm Whatman® 42 filters (Cytiva Life Sciences, Marlborough, MA, USA) at the time the duplicate samples were fumigated. Once extracted, samples were acidified with one drop of DD H₂SO₄. After chloroform fumigation for 24 h in a vacuum desiccator, samples were extracted using the same process as the non-fumigates. Fumigates and non-fumigates were analyzed on a Shimadzu TOC-L Analyzer (Shimadzu Scientific Instruments, Kyoto, Japan) using the non-purgeable organic C base method (detailed analytical procedures are available in Supplementary Table 2). Microbial biomass C (mg kg⁻¹) was calculated as the difference in concentration between fumigated and non-fumigated samples.

2.6. Potential soil CO₂ and CH₄ production

Soil (10 g) from each depth of the core sections were added to a 120 mL serum vial upon return to the laboratory. Any coarse roots were removed from the soil, but the fine roots remained. Vials were crimped-capped with a rubber septum and stored at 4 °C overnight. The following day, vials were evacuated for 1 minute using a vacuum. After evacuation, vials were purged with N₂ gas for 3 min to ensure an anaerobic environment. Then, 16 mL of anaerobic site water filtered through a 0.45-μm Whatman® 42 filter (Cytiva Life Sciences, Marlborough, MA, USA) was added to create the slurry from which potential rates of soil CO₂ and CH₄ production were determined. Site water was made anaerobic before mixing with soil by purging the filtered water with N₂ gas for 20 min. Soil slurries were incubated in an orbital shaker at 25 °C and 150 rpm. Headspace samples were taken with a glass gas-tight syringe every 24 h for five days and immediately analyzed on a Shimadzu GC-2014 equipped with a flame ionized detector (FID) and methanizer (Shimadzu Scientific Instruments, Kyoto, Japan) to determine CO₂ and CH₄ concentrations. Gas production rates were calculated as either CO₂ or CH₄ concentration over time, employing soil pH and Henry’s Law to account for gas in the dissolved phase. The effects of pressure and temperature on gas solubility were calculated with the ideal gas law (Weiss, 1974; See Supplementaty Material for details and equations).

2.7. Data analysis

All sites are referred to as marsh, transition, or mangrove, depending on the dominant vegetation community. Statistical analyses were performed using R version 3.4.1 (RCoreTeam, 2019) within the RStudio “Orange Blossom” 1.2.5033 environment (RStudioTeam, 2020). Data were assessed for normality and homogeneity of variance using the Shapiro-Wilks test and Levene’s test, respectively, and visually via histograms. The R package fitdistrplus (Delignette-Muller and Dutang, 2015) was used to determine each parameter’s best distribution, as almost all parameters, except for pH and moisture content, were non-normally distributed. If two distributions were identified as the best fit, both models were run. The model with the lowest AICc score was chosen. Generalized linear models with a Gaussian or gamma distribution with identity and log links were often used to assist with interpretation. Model structure varied depending on the parameter, which can be seen in Table 2. At first, all parameters were run through an ANCOVA with the following structure: parameter ~ Organic matter proportion (covariate) + River Site + Season + Depth. After running this first complex model, simplified models were run and passed through AICc to determine which terms best fit the model. Type III error was specified in the ANCOVA summaries to reduce the chance of rejecting the null hypothesis for the wrong reason at α = 0.05.
3. Results

3.1. River characteristics

3.1.1. Little Manatee River

Moving downstream from the marsh to the mangrove site, species diversity and herbaceous biomass decreased while canopy cover and woody biomass increased. The vegetation community at the marsh site was dominated by Juncus roemerianus, Typha sp., and Acrostichum danaeifolium, the transition site by J. roemerianus, Typha sp., and A. danaeifolium with Rhizophora mangle seedlings and a single mature R. mangle, and the mangrove site by R. mangle. Average canopy cover at the sites increased from 14.3% at the marsh site (no woody aboveground biomass) to 27.9% at the mangrove site (4.42 Mg ha\(^{-1}\) aboveground woody biomass). Total aboveground biomass was lowest at the marsh site and highest at the transition and mangrove sites (10.2, 25.1, and 21.4 Mg ha\(^{-1}\), respectively; Fig. 2).

Water level deviations were similar among the three sampling sites (Fig. 3A). Generally, the average tidal range increased from the transition (0.36 ± 0.19 m) to the mangrove site (0.44 ± 0.08 m). Surface water salinity measured during the seasonal soil samplings indicated an increase of nearly 6 salinity units between the upstream (marsh) and downstream (mangrove) sites during the dry season (Supplementary Table 2). In contrast, wet season salinity at all sites was less than 1. Weekly salinity was variable during the dry season and early wet season (March–June) at the mangrove site, ranging from 12 in March to 2 at the beginning of June (Fig. 3D). Concentrations of surface water NO\(_x\) were below detection in the dry season and increased to approximately 0.2 mg L\(^{-1}\) in the wet season. Concentrations of NH\(_4^+\) in surface water followed the opposite pattern, decreasing by about 88% in the wet season compared to the dry season. Surface water PO\(_4^{3-}\) concentrations roughly doubled from the dry to the wet season. Generally, surface water DOC concentrations showed no seasonal trends (Supplementary Table 2).

3.1.2. Peace River

The marsh was the only site on the Peace River’s main channel, while the transition and the mangrove sites were both located on Hunters Creek, a braided sub-channel of the main river (Fig. 1). The marsh site was dominated by mixed herbaceous species and A. danaeifolium, the transition site by Schoenoplectus tabernaemontani, Typha sp., and A. danaeifolium with a few R. mangle seedlings, and the mangrove site by R. mangle and A. danaeifolium. Average canopy cover increased moving downstream, from 7.8% at the marsh site to 85.2% at the mangrove site. Woody biomass and canopy cover increased moving downstream. Aboveground total biomass and woody biomass were lowest at the marsh (16.3 and 1.5 Mg ha\(^{-1}\), respectively) relative to the transition (23.1 and 9.5 Mg ha\(^{-1}\), respectively) and mangrove sites (156.5 Mg ha\(^{-1}\); Fig. 2).

Sites displayed similar patterns in water level, tidal range, and salinity fluctuations. Water levels fluctuated seasonally (Fig. 3B). Tidal ranges were also similar (0.39 ± 0.1 m at the mangrove site to 0.45 ± 0.1 m at the transition site). Discrete surface-water salinity measurements indicated a ~ 5-unit increase from the marsh to the mangrove site during the dry season (all sites within the oligo- to mesohaline range), while all sites were fresh (S < 0.5) during the wet season (Supplementary Table 2). Dry season salinity was dynamic at all sites, for example, varying up to 15 within a single week (S = 3–18) at the mangrove site (Fig. 3E).

Across all sites, surface water concentrations of NO\(_x\) were 61, 10.8, or 5.7 times higher in the wet season than the dry season for the marsh, transition, and mangrove sites, respectively. Dry season NO\(_x\) concentrations displayed a slight low-to-high gradient from the marsh to the mangrove site. Season had little effect on both NH\(_4^+\) and PO\(_4^{3-}\) concentrations. Dry season PO\(_4^{3-}\) concentrations decreased slightly from the marsh site to the mangrove site. In the wet season, surface water DOC concentrations were 25–35% lower at the marsh and mangrove sites. The transition site saw a 114% increase in surface water DOC in the wet season (Supplementary Table 2).

3.1.3. Fakahatchee River

Notably, the marsh site was located north of a major highway (US 41, or Tamiami Trail) known to restrict water flow through the Greater Everglades (Krauss et al., 2018). The transition and mangrove sites were located south of US 41. Typha sp. dominated the river channel at the marsh site, Muhlenbergia capillaris dominated the transition site, and the mangrove site was in a stand of Laguncularia racemosa. Neither the marsh site nor the transition site had woody biomass, nor did the mangrove site have herbaceous biomass. Total aboveground biomass was lowest at the marsh and transition sites (42.7 and 44.2 Mg ha\(^{-1}\), respectively) and highest at the mangrove site (Fig. 2). The average canopy cover at the mangrove site was 89.3%, and aboveground woody biomass was 131.8 Mg ha\(^{-1}\).

All three sites experienced a significant dry-down during the 2018 dry season, dipping far below the mean continuous water level recorded during the sampling period (Fig. 3C). At the end of the wet season, water levels at the marsh and the mangrove sites began to fall while rising at the transition site. Average daily ranges in water column depth were small, from 5 ± 8 cm at the marsh and transition to 7 ± 8 cm at the mangrove site and appeared to be driven by evapotranspiration. Of the three sites, the marsh site displayed the greatest difference in salinity between samplings, while the mangrove site had the greatest range in water level fluctuation. Discrete sampling indicated high salinity during the dry season, equivalent to full-strength seawater in the marsh and the transition sites. The mangrove site was brackish, possibly because of a closer hydrologic connection to a constructed ditch along US 41 (Fig. 1; Supplementary Table 2). Continuous salinity data revealed hypersaline conditions (S = −45) at the marsh site in late May 2018.
In contrast, salinity in the wet season was lowest at the transition site and highest at the marsh site (Fig. 3F). Surface water concentrations of DOC, NH$_4^+$, and PO$_4^{3-}$ were similar between sites and seasons. Dry season NO$_x^-$ concentrations were below detection at all sites and increased to 0.05–0.06 mg L$^{-1}$ in the wet season (Supplementary Table 2).

### 3.2. Biogeochemistry

#### 3.2.1. Soil physicochemical properties

Soil OM was most influenced by river and the interaction between river and site ($F = 77.1; p < 0.01$; Table 2). Soil OM concentrations decreased slightly with depth ($F = 19; p < 0.01$), and patterns were non-seasonal. Soil OM content was lowest at the Little Manatee and Peace Rivers and greatest at the Fakahatchee River (Table 1; Fig. 4). Soil DBD decreased with added organic matter ($F = 27.6; p < 0.001$) and generally increased with depth ($F = 10.8; p < 0.001$) (Tables 1 and 2). Organic matter had a strong positive relationship with moisture content ($F = 67.8; p < 0.001$; Table 2). Moisture content was non-seasonal and generally decreased with depth ($F = 5.12; p < 0.01$). Season had the strongest relationship with soil pH ($F = 26.6; p < 0.001$), followed by river ($F = 14.6; p < 0.001$; Table 2). pH was higher in the wet season than in the dry season.

![Fig. 3](image-url)

**Fig. 3.** Deviations from mean annual water level (in meters) (A–C) and mean weekly salinity (in psu) (D–F) for field sites. Error bars are weekly standard deviation. Note different scales on y-axis. For water level, < 0 = dry-down, > 0 = higher than average.

### Table 1

Physicochemical parameters at sites by river and season. Values are averaged over depth ± SE. If season was a significant term in the model, values are separated by season. Trans. = transition and mang. = mangrove.

<table>
<thead>
<tr>
<th>River</th>
<th>Site</th>
<th>Season</th>
<th>Dry bulk density (g cm$^{-3}$)</th>
<th>pH</th>
<th>Moisture content (%)</th>
<th>Soil organic matter (mg kg$^{-1}$)</th>
<th>Total C (mg kg$^{-1}$)</th>
<th>Total N (mg kg$^{-1}$)</th>
<th>Total P (mg kg$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little Manatee</td>
<td>Marsh</td>
<td>Dry</td>
<td>0.29 ± 0.04</td>
<td>6.74 ± 0.1</td>
<td>70.3 ± 2</td>
<td>188 ± 20</td>
<td>107 ± 13</td>
<td>5.7 ± 0.8</td>
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<td></td>
<td></td>
<td>Wet</td>
<td>0.27 ± 0.04</td>
<td>7.00 ± 0.08</td>
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<tr>
<td></td>
<td></td>
<td>Trans.</td>
<td>0.64 ± 0.09</td>
<td>7.06 ± 0.09</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Wet</td>
<td>0.33 ± 0.05</td>
<td>7.32 ± 0.08</td>
<td>61.5 ± 2</td>
<td>105 ± 11</td>
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<td></td>
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<td>Dry</td>
<td>0.81 ± 0.11</td>
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<td></td>
<td>Mang.</td>
<td>Wet</td>
<td>0.81 ± 0.11</td>
<td>7.43 ± 0.09</td>
<td>46.2 ± 2</td>
<td>44 ± 5</td>
<td>26 ± 3</td>
<td>1.1 ± 0.2</td>
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<td>0.79 ± 0.11</td>
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<td>Marsh</td>
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<td>0.63 ± 0.09</td>
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<td>50.8 ± 2</td>
<td>40 ± 4</td>
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<td>1.4 ± 0.2</td>
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<td>Dry</td>
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<td>7.33 ± 0.08</td>
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<td>Peace</td>
<td>Trans.</td>
<td>Wet</td>
<td>0.64 ± 0.09</td>
<td>7.59 ± 0.08</td>
<td>68.1 ± 2</td>
<td>183 ± 19</td>
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<tr>
<td></td>
<td>Mang.</td>
<td>Wet</td>
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<td>75.4 ± 2</td>
<td>260 ± 28</td>
<td>150 ± 17</td>
<td>6.5 ± 0.8</td>
<td>1619 ± 156</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry</td>
<td>0.12 ± 0.02</td>
<td>7.81 ± 0.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Marsh</td>
<td>Wet</td>
<td>0.14 ± 0.02</td>
<td>8.06 ± 0.11</td>
<td>68.5 ± 3</td>
<td>659 ± 70</td>
<td>269 ± 43</td>
<td>20.5 ± 3.7</td>
<td>201 ± 70</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry</td>
<td>0.14 ± 0.02</td>
<td>7.78 ± 0.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fakahatchee</td>
<td>Trans.</td>
<td>Wet</td>
<td>0.13 ± 0.02</td>
<td>8.03 ± 0.1</td>
<td>69.7 ± 3</td>
<td>637 ± 68</td>
<td>282 ± 44</td>
<td>20.5 ± 3.6</td>
<td>466 ± 90</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry</td>
<td>0.13 ± 0.02</td>
<td>8.22 ± 0.08</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mang.</td>
<td>Wet</td>
<td>0.15 ± 0.02</td>
<td>8.47 ± 0.08</td>
<td>74.9 ± 2</td>
<td>425 ± 45</td>
<td>221 ± 27</td>
<td>15.1 ± 2.1</td>
<td>566 ± 54</td>
</tr>
</tbody>
</table>
Fig. 4. Clockwise in each panel: mean potential CH$_4$ production, microbial biomass C, DOC, and potential CO$_2$ production at all rivers. Gray lines are dry season and black lines are wet season. Data are averaged over depth. Error bars represent standard error. Brown bars are the soil organic matter gradients at each river. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
3.2.2. Total and extractable nutrients

Total C ($F = 18.6; p < 0.001$) and N ($F = 20.2; p < 0.001$) generally decreased with depth. Soil OM content had a positive relationship with total C ($F = 18.6; p < 0.001$) and N ($F = 15.4; p < 0.001$) concentrations along all rivers. The Fakahatchee River had the highest average total C and N concentrations out of the three rivers. Soil OM had the strongest relationship with total P concentrations ($F = 58.8; p < 0.001$) along with river ($F = 32.7; p < 0.001$) and the interaction between river and site ($F = 21.1; p < 0.001$). Generally, the Peace River had the highest average total P concentration out of the three rivers studied (Table 1).

All extractable inorganic nutrients were seasonal and had no relationship with soil OM (Table 2). Generally, extractable nutrient concentrations were highest during the dry season (Fig. 5). Neither site alone

Table 2

<table>
<thead>
<tr>
<th>Parameter</th>
<th>OMp</th>
<th>River</th>
<th>Site</th>
<th>Depth</th>
<th>Season</th>
<th>River * Site</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulk density</td>
<td>6.9</td>
<td>15.8</td>
<td>10.3</td>
<td>8.07</td>
<td>22.8</td>
<td>0.81</td>
<td></td>
</tr>
<tr>
<td>Moisture content</td>
<td>5990</td>
<td>4820</td>
<td>7020</td>
<td>1360</td>
<td>1390</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>1.83</td>
<td>15.1</td>
<td>2.49</td>
<td>1.05</td>
<td>3.34</td>
<td>5.58</td>
<td></td>
</tr>
<tr>
<td>Soil OM</td>
<td>85.1</td>
<td>19</td>
<td>9.06</td>
<td>13.6</td>
<td>46.7</td>
<td>0.78</td>
<td></td>
</tr>
<tr>
<td>Total C</td>
<td>4.55</td>
<td>28.4</td>
<td>16</td>
<td>18.8</td>
<td>43.73</td>
<td>0.78</td>
<td></td>
</tr>
<tr>
<td>Total N</td>
<td>4.8</td>
<td>30.6</td>
<td>20.2</td>
<td>18.8</td>
<td>43.73</td>
<td>0.78</td>
<td></td>
</tr>
<tr>
<td>Total P</td>
<td>14.3</td>
<td>15.9</td>
<td>7.98</td>
<td>20.5</td>
<td>0.78</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>Ext. PO₄³⁻</td>
<td>0</td>
<td>169</td>
<td>0</td>
<td>433</td>
<td>475</td>
<td>503</td>
<td></td>
</tr>
<tr>
<td>Ext. NOₓ⁻</td>
<td>-87.7</td>
<td>165</td>
<td>11.7</td>
<td>86</td>
<td>478.88</td>
<td>15.6</td>
<td></td>
</tr>
<tr>
<td>Ext. NH₄</td>
<td>0</td>
<td>1100</td>
<td>0</td>
<td>0</td>
<td>1350</td>
<td>164</td>
<td></td>
</tr>
<tr>
<td>Ext. DOC</td>
<td>8.47</td>
<td>12.5</td>
<td>1.54</td>
<td>2.43</td>
<td>12.4</td>
<td>0.72</td>
<td></td>
</tr>
<tr>
<td>Microbial biomass C</td>
<td>24.86</td>
<td>1.36</td>
<td>2.63</td>
<td>6.42</td>
<td>6.67</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>Pot. CO₂ production</td>
<td>35.9</td>
<td>8.04</td>
<td>4.17</td>
<td>3.82</td>
<td>9.38</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Pot. CH₄ production</td>
<td>195</td>
<td>103.14</td>
<td>0.21</td>
<td></td>
<td></td>
<td>0.12</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 5. Extractable nutrients by point and season at all rivers. Marsh sites are in light gray, transition sites are in dark gray, and mangrove sites are in black. Data are averaged over depth. Error bars are standard error.
nor depth determined extractable PO4-3, and the strongest predictor was season (F = 326; p < 0.001; Table 2). Extractable PO4-3 concentrations increased across the landscape from the Little Manatee River to the Peace and Fakahatchee Rivers. The Little Manatee River marsh site had the highest concentrations during both dry and wet seasons, while the transition and mangrove sites were similar. At the Peace River, extractable PO4-3 concentrations usually increased downstream. The Fakahatchee River was relatively homogenous, with a dry season-low at the transition site to a high at the marsh site. Wet season extractable PO4-3 concentrations were markedly lower and decreased downstream.

Extractable NOx concentrations were highly seasonal (F = 225; p < 0.001), decreased with depth (F = 13.5; p < 0.001), and differed by river (F = 38.9; p < 0.001; Fig. 5; Table 2). Concentrations were up to eight times higher in the dry season than in the wet season (Fig. 5). As with PO4-3, extractable NOx decreased moving downstream at the Little Manatee River. The Peace River’s extractable NOx increased from the marsh to the mangrove site. At the Fakahatchee River, extractable NOx concentrations were generally lowest at the marsh site and peaked at the mangrove site. However, within-site variation was too high to distinguish between sites (F = 2.75; p = 0.07).

Extractable NH4+ concentrations were strongly predicted by season (F = 1350; p < 0.001) and river (F = 1100; p < 0.001; Table 2). Sites along the Little Manatee River had consistently low extractable NH4+, and this nutrient was detectable only during the dry season. The Peace River marsh site had 75% less extractable NH4+ than the transition and mangrove sites during the dry season. Wet season extractable NH4+ were above detection for only the marsh site. Overall, the highest concentrations of extractable NH4+ were at the Fakahatchee River.

Concentrations of DOC were positively correlated with soil OM (F = 8.47; p < 0.001), and patterns differed by river (F = 12.5; p < 0.001) and the interaction between river and site (F = 12.4; p < 0.001). On the Little Manatee River, concentrations were higher and more similar during the dry season and decreased downstream during the wet season (Fig. 4). However, the pattern was reversed at the Peace and Fakahatchee Rivers, where DOC concentrations were higher during the wet season at all sites and increased downstream. The Peace River’s marsh site had the lowest DOC concentrations. The transition site was the highest during the wet season, while the marsh had the highest concentration during the dry season. During the wet season, the local minimum was at the marsh site, and the greatest DOC concentration was found at the mangrove site.

3.2.4. Principal component analysis

PC1 and PC2 explained 48.6% and 16.3% of the variation within the data, respectively (Fig. 6). When data were grouped by vegetation community, there was little difference between the sites (Fig. 6a). The marsh and transition sites overlapped slightly more than either did with the mangrove sites, indicating that the former pair were more like each other than to the mangrove sites. In contrast, significant differences in the data were seen when the PCA was grouped by river (Fig. 6b). Rivers separated along PC1. The Fakahatchee River was characterized by greater soil OM, microbial biomass C, greenhouse gas production, total C and N, and extractable NH4+. Both the Little Manatee and Peace Rivers separated from the Fakahatchee River via increased soil DBD. The Peace River was an intermediate between the other two rivers, as some sites on the Peace River showed intermediate characteristics compared to the other two rivers. Season structured and separated data along PC2 (Fig. 6c) indicating seasonality has a major influence on biogeochemistry. Extractable DOC, pH, and potential CO2 and CH4 production were generally higher in the wet season, while higher concentrations of extractable inorganic nutrients were found in the dry season. The Fakahatchee River’s strong seasonality likely drove this trend.

4. Discussion

We predicted dominant vegetation community (marsh vs. mangrove) would serve as a strong predictor of biogeochemical properties and processes. However, the data revealed more nuanced interactions and, at times, contradicted previously established paradigms. Contrary to our initial prediction, coastal wetland soil biogeochemistry patterns were inconsistent from river to river. Season-directed inorganic nutrient concentrations more than any other predictor in this study.

4.1. Vegetation community was not a robust indicator of salinity

How different ecosystems transition from one species assemble to another in response to sea-level rise depends on the individual species’ salinity tolerance. Some plants, like Taxodium distichum (Krauss et al., 2009) and Sagittaria lancifolia (Howard and Mendelsohn, 1999), show reduced growth with salinity as low as 1.3, while others, such as Scirpus americanus, have a wide salt tolerance (0 < S < 12; Howard and Mendelsohn, 1999). Indeed, S. americanus was found at the transition sites on both the Little Manatee and Peace Rivers, which experienced salinity values between <0.5 and approximately 5 (Supplementary Table 2). Rhizophora mangle dominated the downstream end-member sites on the Little Manatee and Peace Rivers. However, under the canopy, the biogeochemical characteristics were divergent, despite the similar vegetation community and salinity. Therefore, although mangrove encroachment generally increased aboveground biomass at each location, it was not a direct proxy for abiotic conditions.

The expansion of mangroves into previously freshwater marsh has been linked to saltwater intrusion. While mangroves are typically found in saline and brackish environments, they can also establish in freshwater systems, provided that interspecific competition from other mangroves is low. Howard et al. (2015) found that 62–75% of...
A. germinans and L. racemosa survived in freshwater conditions in greenhouse marsh mesocosm single-species plantings. Mangroves located in mesohaline environments along rivers can continue migrating upstream (Yang et al., 2013). Just one long-lasting storm surge that transports a high density of mangrove propagules can shift a previously freshwater marsh to a mangrove forest, as shown by a modeling study of the marsh-mangrove ecotone in the Everglades (Jiang et al., 2014). An extremely dry year followed by an active hurricane season could be enough to transition the freshwater ecosystem to a mangrove swamp.

Based on previous studies, some may assume that mangroves' landward extent coincides with an abiotic salinity and water level threshold. This study found that the mangrove ecotone (transition site) on the Little Manatee and Peace Rivers occurred where salinity averaged approximately 5 during the dry season. However, weekly average salinity converged as wet season rains fell, and all sites on these two rivers became roughly fresh (S < 0.6) from June to September. At the Fakahatchee River during the dry season, saline water (S > 30) was detected 8 km inland from the coast at the marsh and transition sites, while the mangrove site remained brackish in April 2018. Salinity began to decrease in late May at all three sites. The Fakahatchee marsh retained the highest local salinity through the end of the sampling period, which could be due to poor hydrologic connectivity between areas north and south of US 41, a known barrier to water movement in the region (Howard et al., 2017; Krauss et al., 2018).

The marsh-mangrove ecotone is not always the location of biogeochemical intermediates. Generally, the marsh and transition sites were more like each other than either was to the mangrove sites, but this distinction is slight (Fig. 6a). This finding opposes previous research, where the transition zone was more functionally similar to the invading mangrove zone in a salt marsh-mangrove ecotone in Merritt Island, Florida (Steinmuller et al., 2020). This contrast could be because our study was conducted along rivers with multiple channels and modifications, not in a marsh expanse, as in Steinmuller et al. (2020). As mangroves migrate inland via river channels, new mangroves establish in soil formed under herbaceous vegetation. In another Merritt Island study, CO₂ flux was consistently lower from mangrove soils planted with mangrove seedings (A. germinans; 2.91 μg C m⁻² s⁻¹) than from vegetation-free marsh soils (developed under Spartina alterniflora; 8.18 μg C m⁻² s⁻¹) in an experimental mesocosm. Furthermore, soil respiration rates were consistently higher in marsh soils, demonstrating that, upon initial mangrove establishment, CO₂ flux may remain elevated until enough mangrove litter accumulates to change the soil structure (Geoghegan et al., 2021). In contrast, A. germinans soil consistently released more CO₂-C than J. roemerianus soils in field respiration measurements from Tampa Bay, FL (Lewis et al., 2014). Therefore, there may be a lag time between mangrove recruitment and expansion in a previously herbaceous marsh and a quantifiable shift in soil properties due to the new vegetation community.

4.2. Coastal wetland biogeochemical gradients vary across the landscape

Rivers are notoriously variable systems in both time and space (Thoms, 2006). The Little Manatee River was the only location to follow the “classic” coastal wetland soil OM gradient of decreasing OM content with increasing salinity (Chambers et al., 2013; Morrissey et al., 2014; Odum, 1988; Tam and Wong, 1998; Williams et al., 2014; Zhang et al., 2019), with the marsh site having approximately 76% more soil OM than the mangrove site. This river was also the only location with all three sites on the main channel, which may have influenced this trend. However, the mangrove site had the highest soil OM content on the Peace River. Greater boat traffic on the Peace River, both in size and number of boats, may have contributed to increased erosion and soil loss in this system (Mcconchie and Toleman, 2019; Harttung, personal observation). Also, the presence of more mature mangroves on the Peace River may have enhanced the ability of prop roots to act as wave breaks, allowing authigenic OM to accumulate rather than wash...
away (Gedan et al., 2011). Finally, there was no gradient in soil OM content along the salinity/vegetation transect at the Fakahatchee River; the river was relatively homogeneous in soil properties in general.

Soil OM was correlated with many biogeochemical parameters, including moisture content, total C, total N, DOC, microbial biomass C, and potential CO₂ production (Fig. 6a-c). Soils high in OM have an enhanced cation exchange capacity compared to other soils, adsorbing high concentrations of nutrients and releasing them through desorption and decomposition (Capone and Kiene, 1988; Puustjärvi, 1956; Tiessen et al., 1994; Wood et al., 2018). As the interaction between site and river was significant in all models, this evidence that location must be considered when evaluating characteristics of wetland vegetation communities.

4.3. Greenhouse gas production correlates with soil organic matter content across the landscape

The Little Manatee and Peace Rivers displayed opposite patterns of potential CO₂ production, with soil OM explaining the most variation within the model (Table 2). The highly organic mangrove site at the Peace River produced ~3 times more CO₂ than the low soil OM marsh site. At the Little Manatee River, the marsh site’s soil contained the most OM, and CO₂ production was ~2 times higher than from the mangrove site’s soil. The highly organic soils of the Fakahatchee River had order-of-magnitude greater rates of CO₂ production than either of the other two rivers (Fig. 4). In a comparison of storm surge sediment (primarily mineral) and underlying soils (primarily organic) from the same sites in southwest Florida, OM was similarly positively correlated with greater potential CO₂ production (Breithaupt et al., 2020). Soil OM is a major electron donor for microbial respiration in wetland soils. When OM is limited, any areas of high concentration become microbial activity hotspots (Gallardo and Schlesinger, 1994; Hogberg and Ekblad, 1996; Loepmann et al., 2016; Schnürer et al., 1985). Within the soils themselves, nonrandom distribution of roots may have contributed to variability in soil respiration rates, as only rhizomes were removed during incubation bottle preparation.

It has been thought that mangrove ecosystems produce negligible CH₄ because of the increased availability of sulfate in brackish and saltwater systems, as sulfate-reducing bacteria can generally outcompete methanogens for substrate (Alongi et al., 2000, 2001; Bartlett et al., 1987; Capone and Kiene, 1988; Kristensen, 2007; Sotomayor et al., 1994). However, all the transition and mangrove sites in this study produced detectable (0.02–0.1 μg C g⁻¹ h⁻¹) potential CH₄ similar to or higher than their marsh counterparts, despite salinity in the oligo- to mesohaline range (Fig. 4). This phenomenon is likely because of plentiful soil OM, which was positively correlated with CH₄ production. At both the Little Manatee and Peace Rivers, CH₄ production increased downstream. Methane production was maintained even during the dry season salinity peak at the Fakahatchee River, when salinity reached a maximum of 45 at the marsh, indicating the likely presence of sulfate-free microzones (King and Wiebe, 1980) and the existence of non-competitive substrates (Oremland and Polcin, 1982; Winfrey and Zeikus, 1977). The Little Manatee River’s transition site (intermediate salinity) had the maximum CH₄ production among the sites at that river, which has been found in other studies investigating the relationship between salinity and CH₄ production (Paffenbarger et al., 2011). Methane emissions can gradually increase with increasing salinity, until a tipping point between 7 and 10 (Wang et al., 2017), which is a similar range seen at the Little Manatee River during the dry season. In a study examining tidal marshes along an estuarine salinity gradient, the oligohaline site experienced a greater than expected flux of CH₄ during a saltwater intrusion event that increased salinity to around 5.5 (Weston et al., 2014). These results support the idea that factors other than salinity, such as soil OM, can significantly control methanogenesis (Bartlett et al., 1987; Sjögersten et al., 2016; Sotomayor et al., 1994).

4.4. Seasonality and relationships with inorganic nutrient availability and CO₂ flux

Soil extractable nutrient concentrations from all rivers were lower in the wet season across vegetation communities. Wet season concentrations of extractable inorganic nutrients were lower by 87–100% (NOₓ), 71–100% (NH₄⁺), and 94–100% (PO₄³⁻) relative to the dry season. This seasonal pattern could be caused by flushing and dilution during the wet season from Florida’s daily heavy rains (Misra et al., 2018) and by increased plant uptake due to co-occurrence with the growing season (Jonasson and Chapin, 1991; Lee et al., 2013; Picard et al., 2005; Reddy et al., 2000). The relationship between seasonality and surface water nutrients was strong, albeit inconsistently across rivers. NOₓ dominated the speciation of dissolved inorganic N in the Little Manatee River’s surface water in the wet season, while NH₄⁺ was more abundant in the dry season. Increased flow (and less stagnation) during the season of high rainfall and the flux of NH₄⁺ from the soil into the water column with heightened dry season salinity could explain this observation (Jonasson and Chapin, 1991; Luo et al., 2019; Steinmuller and Chambers, 2018; Weston et al., 2010).

However, the Peace River’s surface waters, representing the largest river with the greatest flow, remained dominated by NO₃ year-round. Meanwhile, the Fakahatchee River, a shallow, sheet-flows system, had higher NH₄⁺ than NO₃ in surface water year-round. The dominance of NO₃ at the Peace River and NH₄⁺ at the Fakahatchee River could be related to oxygen availability, as outlined above, as fast-flowing water contains more oxygen than slow or stagnant water (House, 2003).

Concentrations of PO₄³⁻ in surface water doubled from the dry to the wet season at the Little Manatee River. Exceptionally high year-round surface water PO₄³⁻ concentrations (~0.5 mg L⁻¹) were found at the Peace River, where phosphate is naturally plentiful and supports intensive mining activities within this watershed (Filippelli, 2011; Zhang and Ross, 2015). Extractable PO₄³⁻ concentrations at the Fakahatchee River were elevated during the dry season, coinciding with a spike in salinity to ~34 at the “freshwater” marsh, possibly due to the intrusion of ocean water or phosphate desorption from soil particles (Boyer, 2006; Paludan and Morris, 1999; Sundareswar and Morris, 1999).

The Peace River and the Fakahatchee River also showed seasonal variation in CO₂ production but in opposite directions. Generally, CO₂ production increases with oxygen availability, such as during low water periods (Chambers et al., 2013, 2014), as was seen at the Peace River. The Fakahatchee River, on the other hand, had higher CO₂ production during the wet season when water levels were at their highest, which may be due to the extreme saltwater-intrusion event that occurred during the dry season. In this case, the dry season salinity was so high that the additional H₂S produced during sulfate reduction and abundance of Cl⁻ may have stressed the microbial and vegetation communities and reduced metabolic activity (Howes et al., 1981; Lamers et al., 2013; McKee and Mendelssohn, 1989; Mirzoyan and Schreier, 2014; Rath and Rousk, 2015).

5. Conclusion

The most consistent correlate of biogeochemical properties and processes across all three coastal riverine wetlands studied was soil OM content, more so than salinity, plant biomass, or vegetation community (marsh vs. mangrove). This study highlights the high degree of variability among coastal riverine wetland ecosystems, even within a narrow geographic area, and the importance of site-specific investigations over relying on general patterns observed within the literature. Specifically, this study found that 1) soil OM does not always decline across the gradient from freshwater tidal marshes to saltwater mangroves, 2) the vegetation ecotone (transition zone) is not necessarily the site of biogeochemical intermediates (e.g., the transition was more similar to the marsh at the Little Manatee and Fakahatchee Rivers and the mangrove at the Peace River), and 3) methane production can be
highest in mangrove/saline vegetation communities if soil OM content is high. Moreover, the location of the mangrove ecotone does not appear to reflect a specific salinity tipping point. Instead, salinity is dynamic over seasons, with the ecotone being characterized as fresh (S < 0.5) during most of the wet season at all sites and ranging widely (S < 45) during the dry season. Instead of focusing on vegetation communities, we suggest that a simple investigation of soil OM content across a wetland salinity gradient of interest will be the best indicator of various ecologically important biogeochemical properties, including nutrient storage availability and cycling, and greenhouse gas production.

**CRediT authorship contribution statement**

Sarah A. Hartung: conceptualization; data curation; software; formal analysis; investigation; methodology; visualization; writing - original draft; writing - review & editing

Kara R. Radabaugh: data curation; investigation; methodology; writing - review & editing

Ryan P. Moyer: data curation; investigation; methodology; writing - review & editing

Joseph M. Smoak: funding acquisition; writing - review & editing

Lisa G. Chambers: conceptualization; funding acquisition; project administration; resources; supervision; original draft; writing - review & editing

**Declaration of competing interest**

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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**Appendix A. Supplementary data**

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.149056.

**References**


