Increased Organic Carbon Burial in Northern Florida Mangrove-Salt Marsh Transition Zones

Derrick R. Vaughn1,2*, Thomas S. Bianchi1, Michael R. Shields1,3, William F. Kenney4, and Todd Z. Osborne5,6

1Department of Geological Sciences, University of Florida, Gainesville, FL, USA, 2Now at Department of Earth, Ocean, and Atmospheric Sciences, Florida State University, Tallahassee, FL, USA, 3Now at Geochemical and Environmental Research Group, Texas A&M University, College Station, TX, USA, 4Land Use and Environmental Change Institute, University of Florida, Gainesville, FL, USA, 5Whitney Laboratory for Marine Bioscience, University of Florida, St. Augustine, FL, USA, 6Department of Soil and Water Sciences, University of Florida, Gainesville, FL, USA

Abstract: Blue carbon habitats like salt marshes and mangroves bury large amounts of carbon with limited area; however, they also are increasingly susceptible to current climate change. Combined effects of rising temperatures, decreasing freeze frequencies, and increasing sea level rise rates are resulting in mangrove replacement of salt marshes along the southern United States. Surface soils analyzed here from wetlands along northern Florida Atlantic and Gulf Coasts showed higher apparent sedimentation rates in mangrove-dominated sites (1.5–3.2 mm yr⁻¹) and where mangroves are migrating into the marsh (term ed transition sites, 2.3–3.8 mm yr⁻¹). Average carbon burial rates were higher in transition sites for both coasts (27–47 g C·m⁻²·yr⁻¹) compared to the respective mangrove (10–22 g C·m⁻²·yr⁻¹) and salt marsh (4–7 g C·m⁻²·yr⁻¹) sites. Lignin biomarker data (Λ-6, Λ-8, and C/V) indicated that mangrove and transition sites had higher lignin inputs from woody vascular plants compared to salt marsh sites, which may slow decadal-to-centennial-scale decay. Higher amino acid concentrations in mangrove soils relative to salt marsh biomass (1.8–2.3 mmol g C⁻¹ vs. 0.2–0.9 mmol g C⁻¹) and lower C/N indicated that these mangrove sites receive higher algal inputs than the transition and salt marsh sites, attributed to greater tidal inundation in the mangrove sites given their position near the shoreline. Overall, increased accretion, carbon burial, and lignin in mangrove transition sites indicate that this migration may increase carbon burial and increase the stability and residence time of buried soil carbon. Future studies on mangrove migration in northern Florida can verify this through replication and elevation analysis.

1. Introduction

Intertidal mangrove forests and salt marshes are recognized globally as blue carbon ecosystems sequestering and burying large amounts of organic carbon (OC) (Macreadie et al., 2019). This results from high OC production by aboveground and belowground biomass, effective trapping of autochthonous and allochthonous particulate OC, and slower OC catabolism in anoxic soils (Duarte et al., 2005; Mcleod et al., 2011; Windham-Meyers & Troxler, 2019). Average global OC burial rates for mangrove and salt marsh habitats are estimated to be 226 ± 39 g·m⁻²·yr⁻¹ (mean ± one standard error (SE)) and 218 ± 24 g m⁻² yr⁻¹ (Mcleod et al., 2011), respectively. Variability in these estimates is related to variations in plant productivity, aboveground versus belowground biomass, and OC decomposition, all of which are driven by physical (e.g., temperature, sea level, and nutrients) and biological (e.g., species composition, plant competition, and bioturbation) factors (Levine et al., 1998; Mcleod et al., 2011; Alongi, 2014; Herbert et al., 2015).

Florida is second to Louisiana in harboring the largest blue carbon stocks in the United States (Hinson et al., 2017); however, regional climate change impacts have begun to alter these stocks. One potential impact on northern Florida blue carbon stocks is mangrove expansions poleward and inland into salt marshes as temperatures increase and freeze frequency decreases (Saintilan et al., 2014; Cavanaugh et al., 2014; Giri & Long, 2016). Recent Florida mangrove expansion estimates showed mangrove populations doubled along the Atlantic coast (Cavanaugh et al., 2014) and increased ~50% in their northernmost range on the Gulf Coast (Giri & Long, 2016); however, this expansion has not been gradual with multiple periods of mangrove population expansion and contraction (e.g., Cavanaugh et al., 2019; Giri & Long, 2016; Rodriguez et al., 2016). These periods of varying mangrove and salt marsh dominance likely impact soil OC composition and decay...
as much of mangrove biomass is composed of perennial woody structures with abundant lignin-rich material (Hedges & Mann, 1979; Alongi, 2001; Dittmar & Lara, 2001). This contrasts with more grassy salt marsh vegetation that gets recycled annually (Curri et al., 1995).

Globally, mangrove expansion studies document mixed results in carbon sequestration and burial changes with this expansion (e.g., Bianchi et al., 2013; Henry & Twilley, 2013; Kelleway et al., 2016; Perry & Mendelsohn, 2009). A recent study on mangrove expansion into Merritt Island National Wildlife Refuge salt marshes along the central Florida Atlantic coast documented insignificant changes in soil carbon (Doughty et al., 2016). In this study, we assess whether two northern Florida coastlines (Atlantic vs. Gulf Coasts) respond differently to mangrove expansions at similar latitudes. While many of the aforementioned studies focused on separate mangrove and salt marsh sites, this study includes a transitional site where mangroves are actively expanding into salt marshes (mixture of salt marsh and mangrove vegetation) (e.g., Doughty et al., 2016), in addition to separate mangrove- and salt marsh-dominated sites. We hypothesized that mangrove soil OC burial rates would not be significantly higher compared to salt marshes due to the relatively recent mangrove expansion (e.g., Doughty et al., 2016). We also hypothesized higher OC burial rates in the Gulf Coast sites than the Atlantic sites due to lower-energy conditions (e.g., waves and tides), a slightly more gradual sloping coastline, less sediment inputs, and less anthropogenic influences. To examine biogeochemical and sedimentological differences between sites, we used bulk soil carbon/nitrogen, carbon isotopes ($\delta^{13}$C), biomarkers (lignin and amino acids), and geochronological proxies ($^{210}$Pb and $^{137}$Cs).

2. Methods
2.1. Site Description, Collection, and Sample Storage

Two northern Florida coastal wetlands (described in 2.1.1 and 2.1.2) were chosen as representative locations, along the northern Florida Atlantic (St. Augustine) and Gulf (Waccasassa Bay Preserve State Park) Coasts, where mangroves are near their northernmost extent. Both coastal sites, composed of three vegetation habitats (mangrove, salt marsh, and transition), were sampled for biomass estimates and soil analysis. Soils were collected using single 1- to 3-m length vibracores (0.07-m interior diameter, further details in 2.1.4) from each vegetation site (three vibracores per coast, six vibracores total), and biomass estimates (further details in 2.1.3) were made from single 5-m x 5-m plots (three plots per coast, six plots total) centered where vibracores were collected.

2.1.1. Atlantic Coast Site Description

The north Florida Atlantic coast study site is located at Anastasia Island in St. Augustine (Figure 1a). Wetlands here are influenced by semidiurnal tides (~2-m tidal range), flooded by the brackish Matanzas River (Gallivan & Davis, 1981). The river’s hydrodynamics have been altered by water control structures, and dredging is a common sediment source within the estuary, along with soils entrained via tidal forcing (Williams et al., 2014). Additional anthropogenic influences include soil erosion by boat wakes and extensive land-use development.

St. Augustine mangrove populations are composed mostly of *Avicennia germinans* due to its higher low-temperature tolerance (Oslad et al., 2015) with some scattered *Rhizophora mangle*, which produces higher net biomass than *A. germinans* (Lugo et al., 1975). The low intertidal salt marsh is dominated by *Sporobolus alterniflorus* and *Batis maritima*. The transition zone, between mangrove and salt marsh, was dominated by *B. maritima* and *A. germinans*, with some *S. alterniflorus*. Other salt marsh species in the low marsh include *Spartina bakeri*, *Distichlis spicata*, *Salicornia virginica*, and *Sueda* spp.

Northern Florida temperature data (climate division no. 2) [NOAA National Climatic Data Center Time Series, 2018] starting in 1895 indicate local St. Augustine minimum winter temperatures generally increased between 1973 and 2016 (Rodriguez et al., 2016). Relative sea level (RSL) for this region rose 2.6 mm yr$^{-1}$ over the last ~100 yr based on tide gauge data from Mayport, Florida (~72 km north of St. Augustine) (NOAA, 2018).

Since 1942, the beginning of aerial photography in this region, there have been periods of mangrove expansion and contraction into the Anastasia Island salt marsh (Cavanaugh et al., 2014; Rodriguez et al., 2016). The most recent expansion, documented from 2008–2013, resulted in an ~46% mangrove areal extent gain and an ~81% salt marsh loss (Rodriguez et al., 2016). This was likely from winter minimum monthly
temperature increases and less freeze events. In contrast, multiple freeze events occurred between 1980 and 1995, which saw an ~191% mangrove extent decrease and an ~36% salt marsh extent increase (Rodriguez et al., 2016).

2.1.2. Gulf Coast Site Description

Waccasassa Bay Preserve State Park (Figure 1a) along Florida’s Gulf Coast forms the seaward fringe of Gulf Hammock, a formerly vast hardwood forest now composed of salt marshes and coastal forests (Abbott & Judd, 2000). This relatively undeveloped region is characterized as microtidal with low sediment supply and low-energy sea conditions (Geselbracht et al., 2011; Hine et al., 1988; Raabe & Stumpf, 2016). The region also has a relatively stable position with respect to relative sea level rise (RSLR) due to a stable carbonate platform (Geselbracht et al., 2011; Hine et al., 1988; Raabe & Stumpf, 2016); however, since this coastline is lower in elevation and has shallow topographic relief compared to the Atlantic, RSL increases will affect a larger area (DeSantis et al., 2007; Raabe et al., 2004; Raabe & Stumpf, 2016; Williams et al., 1999; Williams et al., 2007). Cedar Key RSLR over the last century (~24 km northwest of Waccasassa Bay study sites) has been 2.1 mm yr\(^{-1}\) [NOAA, 2018]. Minimum temperatures from Cedar Key (Station CDRF1) [NOAA, 2018] between 1995 and 2018 have not increased.

The Waccasassa Bay mangrove population is dominated by *A. germinans*; however, there are many *R. mangle* individuals in the mangrove and transition sites. The Waccasassa Bay salt marsh is dominated by *Juncus roemericanus* and *S. alterniflorus*, along with less common *D. spicata* and *Salicornia* sp. While mangrove expansion studies in Waccasassa Bay are limited, northwestern Florida has experienced past freeze events that limited mangrove extent. This includes a series of freezes during the early 1980s that substantially

Figure 1. (a) Map of Florida (Google Earth, 2019) showing the two northern coastal wetland sites. (b) Vibracore locations in St. Augustine (Google Earth, 2019) in a mangrove vegetation zone (dark blue), a salt marsh vegetation zone (medium blue), and a transition zone (light blue). (c) Vibracore locations in Waccasassa Bay (Google Earth, 2019) in a mangrove vegetation zone (dark red), a salt marsh vegetation zone (medium red), and a transition zone (light red). (d) A zoom in on the salt marsh (medium red) and transition (light red) locations in Waccasassa Bay (Google Earth, 2019).
reduced mangroves and single freezes between the 1960s and 1990s that set back mangrove development by depleting resources (Lugo & Patterson-Zucca, 1977; Montague & Odum, 1997; Stevens et al., 2006).

2.1.3. Estimating Aboveground Biomass
To determine potential influences of aboveground biomass on carbon burial, each site from both coasts was measured for aboveground biomass (B, kg) using single 5-m × 5-m plots centered where vibracores were collected (six plots total; Figures 1b–1d). We sampled the most common mangrove species at the mangrove and transition sites (A. germinans for St. Augustine and Waccasassa Bay and R. mangle for Waccasassa Bay). Each tree was measured for diameter at breast height (DBH, cm, measured 1.3 m above ground), and tree heights were roughly taken to determine whether mangroves were dwarf (<2-m height) or tall (>2-m height). Only heights <2 m were recorded. Trees heights >2 m were designated as tall trees. The number of tall and dwarf trees are in section 3.

Mangrove biomass was estimated using species-specific allometric equations previously used along the Florida Atlantic coast (Simpson et al., 2017); however, future mangrove biomass studies in freeze-prone areas should consider using plant volume-based allometric equations as freezes can affect tree morphology and DBH (e.g., Bulmer et al., 2016; Osland et al., 2014). Dwarf A. germinans biomass was calculated with

$$\log_{10} B = 2.19\log_{10}(DBH) - 3.39$$  \hspace{1cm} (1)

Tall A. germinans mangrove biomass was calculated using

$$\log_{10} B = 1.934\log_{10}(DBH) - 0.395$$  \hspace{1cm} (2)

All R. mangle individuals were dwarf trees, and aboveground biomass estimates were conducted with (Smith & Whelan, 2006):

$$\log_{10} B = 1.731\log_{10}(DBH) - 0.112$$  \hspace{1cm} (3)

Mangrove biomass measurements were multiplied by a 0.48 conversion factor to determine standing tree carbon stock (Kauffman & Donato, 2012). Downed wood, on the ground and in the canopy, was also collected within these plots (Feller et al., 2015). The dead wood was weighed and converted to mean carbon content using a 0.45 conversion factor (Kauffman & Donato, 2012).

A. germinans pneumatophores were collected in a 1-m × 1-m plot (within the 5-m × 5-m plot) for transition and mangrove sites (two plots per coast, four total). Pneumatophore biomass was calculated as dry mass divided by number of pneumatophores (Simpson et al., 2017). Pneumatophore carbon content was calculated by multiplying biomass by a 0.39 conversion factor (Simpson et al., 2017).

Salt marsh vegetation biomass was determined for the salt marsh and transition sites following Kelleway et al. (2016). All salt marsh vegetation, live and dead, was collected in a 30 × 30-cm quadrat (two quadrats per coast, four total), freeze dried, and weighed. Vegetation was not separated by species so a 0.45 conversion factor was applied to estimate carbon content, reflective of S. alterniflorus (Simpson et al., 2017).

2.1.4. Soil Core Collection and Storage
Single 1- to 3-m length vibracores were collected from both coasts at the three separate vegetation sites. Only the top 38 cm of the cores is analyzed here, representing the deepest, modeled 120-yr depth (see section 2.2). Given the likely changes in mangrove and salt marsh extent during soil formation at each vegetation site, this study examines the integrated differences in carbon quantity and quality over their 38-cm and 120-yr profiles. Additionally, single cores are likely more representative of sites over longer timescales (i.e., centennial) compared to short-term timescales (i.e., annual to decadal) (e.g., Breithaupt et al., 2014). Three grab samples (~5 cm deep) from each site were collected randomly in Waccasassa Bay to examine potentially recent soil OC spatial variability. The locations of the sites relative to the shorelines suggest that the mangrove sites would have the most mangrove growth and expansion events in the past, followed by the transition and then salt marsh sites, as mangroves invading salt marsh habitats tend to be restricted to the edges of salt marshes (e.g., McKee & Rooth, 2008).

At the north Florida Atlantic location (St. Augustine, Figure 1b), the geographic coordinates of cores were mangrove (29°43′41″N, 81°14′43″W), salt marsh (29°43′43″N, 82°14′28″W), and transition (29°43′44″N,
81°14′36″W). For the Gulf (Waccasassa Bay; Figures 1c and 1d), the coordinates were mangrove (29°04′39″ N, 82°48′57″ W), salt marsh (29°54′9″ N, 82°49′15″ W), and transition (29°54′7″ N, 82°49′52″ W). Elevation was not collected, though the St. Augustine salt marsh was more characteristic of a low marsh with similar elevation to the mangrove and transition sites. In contrast, the Waccasassa Bay salt marsh was more characteristic of a high marsh, found at a higher elevation than the mangrove and transition sites.

Cores were transported to and stored in a cold room (4 °C) at the University of Florida (UF). Cores were split into 1-m sections with each section split in half, imaged, and subsampled at 2-cm intervals. Samples were collected from the middle of cores to avoid edge effects of plant or topsoil dragged downward as the core penetrated soil. Belowground biomass was not separated or removed (e.g., Breithaupt et al., 2012; Chmura et al., 2003; Smoak et al., 2012) assuming that root biomass turnover continually contributes to soil formation (Castañeda-Moya et al., 2011; Twilley et al., 1992). Soils were weighed, freeze dried, and weighed again to determine bulk density. Volume for bulk density was calculated from multiplying the square of the vibracore’s interior radius (0.035 m) by π and the height of each subsample (0.02 m). Freeze-dried soils were homogenized on a roller mill (Arnold & Schepers, 2004) in precombusted glass bottles with stainless steel rods.

2.2. Development of Age Model

Soil cores were dated down to 40 cm using naturally occurring radionuclides 210Pb (22.3-yr half-life) and 137Cs (30.7-yr half-life). Radionuclide measurements (total 210Pb, 214Bi, 214pb, and 137Cs) were made using low-background gamma counting with well-type intrinsic germanium detectors (Schelske et al., 1994) at UF. Soil ages from 210Pb activities were calculated using two chronology models: constant rate of supply (CRS) and constant flux, constant sedimentation (CFCS) (Appleby & Oldfield, 1978; Krishnaswamy et al., 1971), with SE reported based on uncertainties in the radionuclide counts and in the assigned dates (Appleby, 2001). Because 210Pb dating is typically limited to sediments <5 half-lives old, analysis of each core was limited to the 120-yr age horizon (Breithaupt et al., 2012). Additionally, since excess 210Pb (210Pbex) can be influenced by clay adsorption (Chanton et al., 1983; Cundy & Croudance, 1995), a correction was applied to 210Pbex to correct for clay content variability. This correction was based on 40K activity, a natural isotope used as a clay concentration indicator (Doveton, 1994; Olsen et al., 1989). Once chronologies were established, confidence in 210Pbex chronologies can increase when comparing to 137Cs peaks within core profiles, hypothesized to represent peak 137Cs deposition from nuclear bomb testing in 1963 (Krishnaswamy et al., 1971).

Both CRS and CFCS are commonly used in mangrove (e.g., Breithaupt et al., 2014; Ruiz-Fernández et al., 2018) and salt marsh (e.g., Haslett et al., 2003; Schuerch et al., 2016) sedimentation studies, and they are used here to compare apparent sedimentation rates; however, the assumptions of constant 210Pbex fluxes for both models and of constant sedimentation for CFCS have likely been compromised at these sites (see section 3.2). Unlike CFCS, CRS accounts for past variations in sedimentation rates. A third less commonly used model, constant initial concentration, was not used as it assumes constant sedimentation and requires simultaneous compaction measurements (Robbins & Edgington, 1975).

The deepest 120-yr age horizon was at 38 cm for the Waccasassa Bay mangrove core (shallowest in Waccasassa salt marsh at 4 cm) using the CFCS model; thus, all downcore analyses were done to each core’s 38-cm depth. By analyzing the top 38 cm, as opposed to 120-yr records, we provided more uniform and integrative comparisons of geochemical parameters between vegetation sites (albeit temporal differences among cores). Some 120-yr records also did not produce enough data for significant testing (e.g., one data point for biomarker data within the Waccasassa salt marsh 120-yr CFCS and CRS records), which would have hindered our assessments.

2.3. Bulk Soil Carbon and Nitrogen Analyses

Soil samples from the top 38 cm of each core were analyzed for total organic carbon (TOC), total nitrogen, and for stable carbon isotopes using a Carlo Erba 1500 CN elemental analyzer coupled to a Thermo Electron DeltaV Advantage isotope ratio mass spectrometer in UF’s Department of Geological Sciences. Before TOC analysis, soils were fumigated (Harris et al., 2001) with 12-M HCl for 8 hr to remove inorganic carbon. OC and nitrogen concentrations are reported as percentages of dry soil, while stable isotope data are reported...
in $\delta^{13}C$ (‰) notation relative to the Vienna Pee Dee Belemnite standard. C/N is based on the molar ratio of TOC to total nitrogen.

Total carbon stock over 120-yr and 38-cm intervals was calculated using

$$\text{Core Stock} \left( \frac{\text{kg}}{\text{m}^2} \right) = \sum_{n} \left( \frac{\text{TOC}_n}{100} \times \text{bulk density}_n \left( \frac{\text{kg}}{\text{m}^3} \right) \times \text{sampling interval (m)} \right)$$

(4)

TOC (%) from each sample ($n$) making up the 120-yr and 38-cm intervals was divided by 100%, with the sampling interval representing the length of core subsamples (0.02 m). Dividing the 120-yr core stock by the bottom age of the $^{210}$Pb models provided estimates of average carbon burial rates. A mean relative standard deviation of 5% was applied to the core stock based on a 1-mm error in subsampling a 2-cm section (Shields et al., 2017).

2.4. Lignin Oxidation and Analyses

Lignin phenols were extracted and analyzed using a modified cupric oxide method (Hedges & Ertel, 1982; Louchouarn et al., 2010), reported in detail in Shields et al. (2019). Total lignin was quantified as the summation of vanillyl (V), syringyl (S), and cinnamyl (C) phenols normalized to 100 mg of OC ($\Lambda$-8). Similarly, $\Lambda$-6 represents the summation of V and S phenols normalized to 100 mg OC. Since lignin is found almost exclusively in terrestrial plants (Ertel et al., 1984; Ertel & Hedges, 1984, 1985; Hedges & Mann, 1979; Hedges & Oades, 1997), total lignin represents relative vascular plants inputs to soil OC. C/V and S/V are often used to indicate lignin sources (Hedges et al., 1988), where V phenols are ubiquitous among plant tissues and types, C phenols are primarily from soft tissues (grasses and leaves), and S phenols are primarily from angiosperms. Thus, C/V estimates nonwoody versus woody contributions and S/V separates angiosperm and gymnosperm contributions (Ertel & Hedges, 1984). Oxidative degradation of lignin by fungi and other microbes can, however, alter these ratios (Hedges et al., 1988; Jex et al., 2014; Opsahl & Benner, 1995). To better understand the degradation state of lignin, acid-to-aldehyde ratios of V and S phenols ((Ad:Al)$_{V}$ and (Ad:Al)$_{S}$, respectively) were measured. (Ad:Al)$_{V}$ in fresh tissues is typically <0.3 and is >0.6 in highly degraded material (Hedges et al., 1998). (Ad:Al)$_{S}$ in fresh tissues and highly degraded tissues have ratios <0.14 and > 0.16, respectively (Hedges et al., 1998).

2.5. Amino Acids

Amino acids were analyzed using methods in Hutchings et al. (2018). Nineteen amino acids were detected and quantified: hydroxyproline (Hyp), serine (Ser), glycine (Gly), aspartic acid (Asp), threonine (Thr), glutamic acid (Glu), alanine (Ala), proline (Pro), gamma-amino butyric acid (GABA), muramic acid (MurA), valine (Val), Diaminopimelic acid (DAPA), tyrosine (Tyr), histidine (His), lysine (Lys), isoleucine (Ile), leucine (Leu), arginine (Arg), and phenylalanine (Phe). The average instrumental relative standard deviation for compounds was 10%, ranging from 7% (Pro) to 14% (Gly).

Amino acids form the building blocks of proteins and are more ubiquitous than lignin, making them more representative of total soil organic matter. Total hydrolysable amino acids (THAA) sums the 19 amino acids normalized to OC. The percentage of which amino acids made of the total nitrogen pool (AA N%) was calculated using (Philben et al., 2014):

$$AA_N = \sum \left( \frac{\text{Yield}_{AA}}{N} \right) \times \text{Wt} \% (N)_{AA}$$

(5)

where Yield$_{AA}$/N is the N-normalized concentration of an amino acid in mg AA (100 mg N)$^{-1}$ and Wt%$(N)_{AA}$ is the weight %N in the amino acid.

The mole percent of each amino acid was used in a principal component analysis (PCA; Figure S4 in the supporting information) to generate an amino acid degradation index (DI) (Dauwe et al., 1999; Philben et al., 2016):
Samples used to develop the DI index came from soil found throughout the cores (1–3 m) collected at each site, not just the 38-cm intervals here. Within the DI equation, $Var_i$ is the mole percent of each amino acid, $Avg_i$ is the mean of the amino acids in the data set, and $SD_i$ is the standard deviation of the amino acids. $PC_{1i}$ represents the score of the amino acids on the first principal component axis. Lower DI values indicate more degraded or altered soils.

Carbon-normalized concentration of individual amino acids can also indicate OC sources to the soil. Hyp is found in plant structural proteins and in some algae (Gotelli & Cleland, 1968; Kieliszewski & Lamport, 1994; Philben & Benner, 2013) and tends to increase with decomposition (Philben & Benner, 2013). Amino acids MurA and DAPA have been used as bacterial OC indicators, while GABA is often used as an OC diagenetic state indicator (e.g., Hutchings et al., 2019; Philben et al., 2016).

2.6. Statistical Testing

Statistical testing was used to determine whether measured parameters were significantly different between core profiles collected from three different vegetation sites along the two coastlines. We acknowledge the statistical limitations associated with collecting single vibracores from each site and have tested the values generated within the 38-cm core profiles for significance using a balanced bootstrap approach with 10,000 iterations using the statistical computing software R (R Core Team, 2019). This gives 95% confidence intervals (CI) of the bootstrapped means for each core profile. Values within core profiles are considered significantly different if their 95% CI do not overlap, equivalent to a $p$ value < 0.05. The bulk and biomarker parameters were also tested for significant changes against each other and over the 38-cm records using a linear regression model. $R^2$ values are reported for those with significant changes ($p$ values < 0.05).

3. Results

3.1. Aboveground Biomass and Carbon Concentrations

3.1.1. St. Augustine

The mangrove site consisted of tall ($n = 30$) and dwarf ($n = 7$) $A$. germinans and had the highest aboveground biomass and C concentration with $1.1 \times 10^3$ kg m$^{-2}$ and $5.4 \times 10^2$ kg C m$^{-2}$, respectively. The transition site had a smaller biomass and C concentration of $9.3$ kg m$^{-2}$ and $4.2$ kg C m$^{-2}$, respectively, consisting of dwarf $A$. germinans ($n = 46$) and salt marsh vegetation. The low salt marsh site had the lowest biomass and C concentration, with $9.0$ kg m$^{-2}$ and $4.0$ kg C m$^{-2}$, respectively.

3.1.2. Waccasassa Bay

The mangrove site had the highest aboveground biomass and C concentration at $1.2 \times 10^4$ kg m$^{-2}$ and $5.9 \times 10^5$ kg C m$^{-2}$, respectively. The mangrove site trees were only $A$. germinans, with 41 tall and 17 dwarf. In contrast, the transition was dominated by dwarf $R$. mangle ($n = 58$) with some tall $A$. germinans ($n = 5$). Total aboveground biomass and C concentration estimates in the transition site were $2.5 \times 10^3$ kg m$^{-2}$ and $1.2 \times 10^3$ kg C m$^{-2}$, respectively. The high salt marsh site recorded the lowest aboveground biomass and C concentration with $93$ kg m$^{-2}$ and $42$ kg C m$^{-2}$, respectively.

3.2. Geochronology

Most $^{210}$Pb$_{ss}$ profiles demonstrated exponential decreases over depth (Figure S1). Waccasassa Bay $^{210}$Pb$_{ss}$ activities (6.9 to 7.4 dpm g$^{-1}$) were higher compared to St. Augustine (2.7 to 4.1 dpm g$^{-1}$, Figure S1). Ages ($\pm 1$ SE) and depths closest to the 120-yr limit for $^{210}$Pb$_{ss}$ models based on the CFCS model (CRS model) in St. Augustine were $87 \pm 49$ yr at 24 cm (106 $\pm$ 23 yr at 16 cm), $107 \pm 84$ yr at 10 cm (86 $\pm$ 43 yr at 8 cm), and $95 \pm 28$ yr at 26 cm (86 $\pm$ 15 yr at 20 cm) for the mangrove, salt marsh, and transition cores, respectively. The ages and depths for the mangrove, salt marsh, and transition sites in Waccasassa Bay were $119 \pm 24$ yr at 38 cm (113 $\pm$ 22 yr at 34 cm), $103 \pm 497$ yr at 4 cm (119 $\pm$ 148 yr at 4 cm), and $83 \pm 33$ yr at 34 cm (105 $\pm$ 21 yr at 26 cm), respectively. Apparent sedimentation rates (reported with $\pm 1$ SE) were calculated from the linear regression of the natural log of $^{210}$Pb$_{ss}$ (corrected to $^{40}$K to adjust for variable clay content) and the middepth cumulative mass (Nitttrouer & Sternberg, 1981) over the 120-yr ages reported above (e.g., $87 \pm 49$ yr for St. Augustine mangrove CFCS model), with error determined from the 95% CI of the
regression’s slope. In St. Augustine, apparent sedimentation rates based on the CFCS (CRS) model were 2.8 ± 2.1 mm yr\(^{-1}\) (1.5 ± 0.3 mm yr\(^{-1}\)), 0.9 ± 0.3 mm yr\(^{-1}\) (0.9 ± 0.3 mm yr\(^{-1}\)), and 2.7 ± 1.1 mm yr\(^{-1}\) (2.3 ± 0.3 mm yr\(^{-1}\)) for the mangrove, low salt marsh, and transition sites, respectively. Waccasassa apparent sedimentation rates based on the CFCS (CRS) model for the mangrove, high salt marsh, and transition sites were 3.2 ± 1.4 mm yr\(^{-1}\) (3.0 ± 0.5 mm yr\(^{-1}\)), 0.4 ± 0.3 mm yr\(^{-1}\) (0.3 ± 0.2 mm yr\(^{-1}\)), and 3.8 ± 1.4 mm yr\(^{-1}\) (2.7 ± 0.5 mm yr\(^{-1}\)), respectively.

Inventories of \(^{210}\)Pb\(_{\text{ex}}\) were all below the global mean inventory (~35.5 dpm cm\(^{-2}\)) (Nozaki et al., 1978), implying low \(^{210}\)Pb\(_{\text{ex}}\) delivery, a delivery hiatus, and/or loss of soil. St. Augustine (Waccasassa Bay) inventories were 4.6 dpm cm\(^{-2}\) (4.6 dpm cm\(^{-2}\)), 1.7 dpm cm\(^{-2}\) (1.5 dpm cm\(^{-2}\)), and 3.2 dpm cm\(^{-2}\) (6.2 dpm cm\(^{-2}\)) in the mangrove, salt marsh, and transition sites, respectively. Natural log of \(^{210}\)Pb\(_{\text{ex}}\) activity plotted against depth created a best fit linear regression model (Figure S1), showing that mangrove and transition sites had low to moderate correlations between the two variables, whereas the salt marsh sites had high correlation. Low to moderate correlation may suggest that there were variable \(^{210}\)Pb\(_{\text{ex}}\) fluxes to the mangrove and transition sites, variability in sedimentation rates, or some \(^{210}\)Pb\(_{\text{ex}}\) mixing from crab bioturbation and/or wave/tidal physical mixing. Similar correlations between both coasts may suggest that dredging in St. Augustine had minimal impact on \(^{210}\)Pb\(_{\text{ex}}\).

Waccasassa Bay and St. Augustine \(^{137}\)Cs activities ranged from 0.6 to 1.3 dpm g\(^{-1}\) and 0.2 to 1.1 dpm g\(^{-1}\), respectively (Figure S1). Three sites did not show \(^{137}\)Cs peaks that could validate the \(^{210}\)Pb. The Waccasassa Bay transition \(^{137}\)Cs peak was below the 120-yr records determined by the CFCS and CRS models and was thus not used to calculate apparent sedimentation rates. This deeper peak and lack of \(^{137}\)Cs peaks in other cores may relate to \(^{137}\)Cs mobility in anoxic sediments and its migration through the sediment column (Crusius & Anderson, 1991; Kenney et al., 2016). The other two profiles with \(^{137}\)Cs peaks were the St. Augustine transition and Waccasassa Bay mangrove. The \(^{137}\)Cs peak in the Waccasassa Bay mangrove was near the 1963 age marker from both CFCS and CRS, whereas the \(^{137}\)Cs peak in the St. Augustine transition was above the 1963 age marker of both \(^{210}\)Pb models. Apparent sedimentation rates calculated from \(^{137}\)Cs were 1.5 mm yr\(^{-1}\) for the St. Augustine transition and 4.0 mm yr\(^{-1}\) for the Waccasassa Bay mangrove.

### 3.3. TOC, C/N, and \(\delta^{13}C\)

TOC was significantly highest in the Waccasassa Bay transition over 38 cm compared to all other Waccasassa Bay and St. Augustine sites (Table S1). Waccasassa mangrove had the second highest TOC, significantly larger than the St. Augustine mangrove and both salt marsh sites. TOC in grab samples collected from Waccasassa Bay was also the highest in the transition (range 10.6–14.4%) compared to the mangrove (8.4–10.8%) and the high salt marsh (7.6–12.1%). Within St. Augustine, the transition 38-cm TOC was significantly higher than the low salt marsh and mangrove TOC. TOC significantly increased from depth to the surface in all St. Augustine sites (mangrove \(R^2 = 0.39\), low salt marsh \(R^2 = 0.50\), transition \(R^2 = 0.91\)) (Figure 2). TOC also increased significantly up-core in all Waccasassa Bay sites (mangrove \(R^2 = 0.56\), high salt marsh \(R^2 = 0.53\), and transition \(R^2 = 0.67\)) (Figure 2).

C/N was significantly the highest in the St. Augustine transition compared to all St. Augustine and Waccasassa Bay sites over 38 cm (Table S1). C/N within Waccasassa Bay was significantly higher in the high salt marsh compared to the transition and mangrove. The Waccasassa Bay end-members with the lowest C/N included green algae and the A. germinans and R. mangle leaves from the mangrove site, whereas the lowest St. Augustine end-member C/N values were in S. alterniflora and B. maritima leaves (Table S2). C/N decreased significantly up-core in the St. Augustine mangrove (\(R^2 = 0.83\)) and transition (\(R^2 = 0.49\)), as well as in the Waccasassa Bay transition (\(R^2 = 0.53\)).

The Waccasassa Bay transition was significantly more \(^{13}C\) enriched over 38 cm compared to all sites from both coasts (Table S1). Within St. Augustine, the low salt marsh was more \(^{13}C\) enriched than the mangrove and transition. Over the 38-cm interval, the depletion in the St. Augustine \(^{13}C\) mangrove record (\(R^2 = 0.80\)) and the enrichment in the St. Augustine low salt marsh and Waccasassa Bay mangrove \(^{13}C\) records (\(R^2 = 0.55\) and 0.74, respectively) were significant (Figure 2).
3.4. Average Carbon Burial Rates

Based on the 38-cm and 120-yr records and the percent carbon, carbon stocks and average carbon burial rates were higher for Waccasassa Bay than St. Augustine (Table 1). The salt marsh sites are the only exception, where the St. Augustine low salt marsh buried more carbon than the Waccasassa Bay high salt marsh. Both coasts showed the transition burying the most carbon, whereas the salt marsh buried the least.

Table 1
Carbon Stocks (kg C m⁻² ±5% RSD) in the St. Augustine and Waccasassa Bay Sites for Both the 120-yr Marker and the 38-cm Profiles Along With Carbon Burial Rates (g C m⁻² yr⁻¹ ±1 SE) for the St. Augustine and Waccasassa Bay Sites as Well as Global Average Burial Rates for Salt Marshes and Mangroves (±1 SE) (Mcleod et al., 2011)

<table>
<thead>
<tr>
<th>Sites</th>
<th>120-yr carbon stock CFCS (top) CRS (bottom) (kg C m⁻²)</th>
<th>38-cm carbon stock (kg C m⁻²)</th>
<th>Carbon burial rates CFCS (top) CRS (bottom) (g C m⁻² yr⁻¹)</th>
<th>Global average carbon burial rates (Mcleod et al., 2011) (g C m⁻² yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>St. Augustine Salt Marsh</td>
<td>0.74 ± 0.04</td>
<td>2.47 ± 0.12</td>
<td>7 ± 1</td>
<td>218 (±24)</td>
</tr>
<tr>
<td>St. Augustine Mangrove</td>
<td>0.57 ± 0.03</td>
<td>2.44 ± 0.12</td>
<td>17 ± 6</td>
<td>226 (±17)</td>
</tr>
<tr>
<td>St. Augustine Transition</td>
<td>1.09 ± 0.05</td>
<td>4.18 ± 0.21</td>
<td>34 ± 15</td>
<td>226 (±17)</td>
</tr>
<tr>
<td>Waccasassa Bay Salt Marsh</td>
<td>0.52 ± 0.03</td>
<td>2.98 ± 0.15</td>
<td>5 ± 4</td>
<td>218 (±24)</td>
</tr>
<tr>
<td>Waccasassa Bay Mangrove</td>
<td>0.52 ± 0.03</td>
<td>2.76 ± 0.14</td>
<td>22 ± 10</td>
<td>226 (±17)</td>
</tr>
<tr>
<td>Waccasassa Bay Transition</td>
<td>3.87 ± 0.19</td>
<td>4.30 ± 0.22</td>
<td>47 ± 19</td>
<td>47 ± 19</td>
</tr>
<tr>
<td></td>
<td>3.27 ± 0.16</td>
<td></td>
<td>31 ± 7</td>
<td></td>
</tr>
</tbody>
</table>
3.5. Lignin Phenols

Total lignin normalized to OC (Λ 6 and Λ 8; Table S3) was not significantly different within the 38 cm between coasts, with the highest occurring in the low salt marsh for St. Augustine (not significant) and in the transition for Waccasassa Bay (significantly greater than salt marsh but not mangrove). Both coasts recorded total lignin values similar to those of their respective end-members (Table S4). Over the 38-cm intervals, only the St. Augustine transition and low salt marsh significantly increased ($R^2 = 0.77$ and 0.48 for Λ 6, respectively; Figure S2) ($R^2 = 0.63$ and 0.54 for Λ 8, respectively; Figure 3). In contrast, Λ 6 in the Waccasassa Bay transition significantly decreased ($R^2 = 0.52$).

Within St. Augustine, both degradation parameters (Ad/Al)$_v$ and (Ad/Al)$_s$ were significantly higher for the 38-cm transition record compared to the low salt marsh and mangrove (Table S3). For Waccasassa Bay, (Ad/Al)$_v$ was not significantly different between sites and (Ad/Al)$_s$ was significantly higher in the high salt marsh compared to the transition; however, the mangrove site had the highest (Ad/Al)$_s$. Both degradation parameters in St. Augustine had values similar to the collected end-members, whereas the Waccasassa Bay (Ad/Al)$_v$ values were higher than most end-members and (Ad/Al)$_s$ values were lower than most end-members (Table S4). Both sites, however, had ratios between what would be expected for fresh litterfall (($Ad/Al)_v < 0.13$ and (Ad/Al)$_s < 0.3$) and highly degraded lignin (($Ad/Al)_v > 0.16$ and (Ad/Al)$_s > 0.6$) (Hedges et al., 1998). Comparing (Ad/Al)$_v$ and (Ad/Al)$_s$ between sites showed that the St. Augustine transition and mangrove ($R^2 = 0.85$ and 0.93, respectively) and the Waccasassa Bay mangrove and high salt marsh ($R^2 = 0.80$ and 0.89, respectively) were positively correlated. This suggested that both phenol groups are degraded at similar rates. Over the 38-cm interval, only the St. Augustine transition and low salt marsh had significant decreases in (Ad/Al)$_v$ ($R^2 = 0.83$ and 0.57, respectively; Figure 3).

C/V over 38 cm was significantly highest in the low salt marsh and transition for St. Augustine and in the high salt marsh for Waccasassa Bay (Table S3). St. Augustine woody and nonwoody end-members yielded high C/V ratios, while *A. germinans* stem in Waccasassa Bay had the lowest C/V ratio from both coasts (Table S4). S/V ratios in all samples for both coasts were greater than one. Over the 38-cm interval, only the salt marsh sites for both coasts significantly increased in C/V ($R^2 = 0.57$ and 0.59 for St. Augustine and Waccasassa Bay, respectively; Figure 3).

3.6. Amino Acids

Total amino acids (THAA, Table S5) over 38 cm was significantly higher in the mangrove sites for both coasts compared to the salt marshes; however, mangrove THAA was only significantly higher than the transition in St. Augustine. The St. Augustine mangrove end-members mostly had lower THAA compared to salt marsh vegetation, while Waccasassa Bay mangrove end-members had higher or equal amounts of THAA compared to salt marsh and algal end-members (Table S6). THAA over the 38-cm intervals in St. Augustine decreased significantly to the surface for the transition ($R^2 = 0.37$; Figure 4). The increase in THAA for the Waccasassa Bay high salt marsh was significant ($R^2 = 0.62$).

The contribution of amino acid nitrogen to the total nitrogen (AA N%, Table S5) was not significantly different between Waccasassa Bay sites over 38 cm but was significantly higher in the St. Augustine mangrove compared to the low salt marsh. AA N% was also significantly higher in the Waccasassa Bay mangrove compared to all St. Augustine sites. The AA N% in the soils for both coasts was mostly lower than the end-members, except for *A. germinans* in St. Augustine (Table S6). Over the 38-cm interval, St. Augustine AA N% significantly decreased for the transition ($R^2 = 0.67$; Figure S3). Waccasassa Bay AA N% increased significantly over this interval for the mangrove site ($R^2 = 0.57$).

The amino acid DI was significantly higher in the St. Augustine transition over 38 cm compared to the respective low salt marsh and mangrove sites (Table S5). Similarly, the Waccasassa Bay mangrove had significantly higher DI compared to the high salt marsh but not to the transition. Almost all soil samples from both coasts had DI values lower than the end-members (Table S6). There were no significant changes in DI for the St. Augustine sites; however, the Waccasassa Bay DI increased significantly up-core for the mangrove site ($R^2 = 0.63$; Figure 4).

GABA, often used to indicate amino acid decay, was significantly higher in the 38 cm mangrove and salt marsh records compared to the transition for both coasts (Table S5). While GABA was found in *A.
germinans end-members in St. Augustine, it was either not detected or barely detected in Waccasassa Bay mangrove end-members (Table S6). Conversely, some high salt marsh vegetation in Waccasassa Bay had high GABA concentrations, whereas GABA concentrations in St. Augustine low salt marsh vegetation were not detected. Our analytical method used to quantify amino acids does not distinguish GABA from its isomers, alpha- and beta-aminobutyric acid (Hutchings et al., 2018), which can be present in plant tissues. Hyp, used as an indicator for plant contributions to soil organic nitrogen, was significantly the highest in mangrove sites for both coasts over 38 cm compared to salt marsh sites (Table S5). Hyp concentrations were high for A. germinans end-members for both coasts (Table S6), whereas only some salt marsh vegetation produced high concentrations. Hyp increased significantly over the 38-cm interval for the St. Augustine transition and mangrove sites ($R^2 = 0.92$ and $0.52$, respectively; Figure 4), as well as in the mangrove site for Waccasassa Bay ($R^2 = 0.42$).

DAPA and MurA, both used to indicate bacterial contributions, were mostly not significantly different between coasts (Table S5). MurA was not detected in any St. Augustine end-members but was detected in Waccasassa Bay algae and B. maritima. DAPA was also low in all St. Augustine vegetation and was only present in Waccasassa Bay algae and B. maritima belowground end-members (Table S6).

4. Discussion

4.1. Higher Apparent Sedimentation in Salt Marsh to Mangrove Transitions

4.1.1. Potential Mechanisms for Increased Apparent Sedimentation

Apparent sedimentation rates calculated from $^{210}$Pb activity (limited to 120 yr) were highest for mangrove and transition sites of both coasts using the CFCS and CRS models. St. Augustine mangrove and transition sites had CFCS (CRS) rates of $2.8 \pm 2.1$ mm yr$^{-1}$ ($1.5 \pm 0.3$ mm yr$^{-1}$) and $2.7 \pm 1.1$ mm yr$^{-1}$.
Waccasassa Bay mangrove and transition sites had CFCS (CRS) rates of 3.2 ± 1.4 mm yr⁻¹ (3.0 ± 0.5 mm yr⁻¹) and 3.8 ± 1.4 mm yr⁻¹ (2.7 ± 0.5 mm yr⁻¹), respectively. These apparent sedimentation rates represent net sediment accumulation over the last ~120 yr and thus do not detail how sedimentation has changed within this period. This is important to note as mangroves have expanded and contracted in both wetlands during this time, which may have altered sedimentation rates. Although mangrove and salt marsh changes have been well documented from aerial photographs for St. Augustine (e.g., Rodríguez et al., 2016), we are unable to compare these vegetation changes to ²¹⁰Pb dates as there are annual-to-decadal-scale uncertainties in the dates that become larger with depth.

Higher sedimentation rates are achieved from higher mineral and organic sediment inputs, which are influenced by plant biomass and density, flooding tidal frequency, suspended sediment and OC concentrations in floodwaters, and distance from tidal sources (Chmura et al., 1994; Day et al., 1999; Morris et al., 2002; McKee et al., 2007; Kirwan & Murray, 2007; Kirwan & Megonigal, 2013). Although sediment inputs were not measured, mineral sediment deposition was likely highest in sites closest to the shorelines (i.e., the mangrove sites) as suspended mineral sediments from tidal flooding settle closer to the wetland edge (Stumpf, 1983).

Mangroves within the mangrove and transition sites today and from previous expansions also had/would have had more complex and denser aboveground, and possibly belowground, biomass structures that bind and trap more mineral sediments from runoff and tidal exchange compared to the salt marsh vegetation that dominates the salt marsh sites (Comeaux et al., 2012; Scoffin, 1970). Waccasassa Bay mangroves are currently taller than St. Augustine mangroves and thus may have captured more mineral and organic sediment, leading to higher apparent sedimentation rates for Waccasassa Bay mangrove and transition sites compared to the same sites in St. Augustine. A previously established positive correlation between mangrove tree height and belowground biomass (Yando et al., 2018) may also suggest that there was more belowground biomass in Waccasassa Bay that could increase sediment capture and soil elevation. Many environmental variables could have induced mangrove height differences between coasts, including differences in air...
temperatures, freeze events, precipitation, physical coastal processes (e.g., lower tidal/wave energy along the Gulf compared to the Matanzas River), salinity, nutrient availability, flooding frequency, surface hydrology, oxidation-reduction status of the soil, and sulfide concentrations (Feller et al., 2003; Krauss et al., 2006; McKee et al., 2007; Reef et al., 2010).

In contrast to the mangrove and transition sites, salt marsh apparent sedimentation rates were higher in St. Augustine. This likely resulted from the Waccasassa Bay marsh site being in the high marsh compared to the low marsh in St. Augustine, with less mineral sediments and possibly less mangrove individuals from past mangrove expansions reaching high marsh elevations compared to low marsh elevations (McKee & Rooth, 2008; Stumpf, 1983). Additionally, the Waccasassa Bay high salt marsh currently had lower biomass that may suggest that this salt marsh has less organic matter to contribute through litterfall.

Using lower apparent sedimentation rates of the CRS model, to be conservative, most apparent sedimentation rates suggest that these mangrove and transition sites are currently keeping up with centennial RSLR rates for these regions (Mayport RSLR = 2.6 mm yr$^{-1}$; Waccasassa RSLR = 2.1 mm yr$^{-1}$; NOAA, 2018). Increases in RSLR rates over the last century may have increased sedimentation rates at these sites as wetlands adjust their elevation in response to RSLR through the creation of vertical accommodation space, promoting mineral and organic sediment accumulation (Morris et al., 2002; Rogers et al., 2019). Additionally, aboveground and belowground vegetation productivity can increase in response to RSLR (Morris et al., 2002), resulting in potentially increased OC availability from litterfall. Future RSLR rate increases may increase sedimentation rates from higher productivity and mineral and organic sediment accumulation; however, when RSLR rates exceed sedimentation rates, the shoreline sides of these wetlands (i.e., the mangrove sites) would become more susceptible to drowning and elevation loss (e.g., Krauss et al., 2010). Additionally, wetland transgression in response to RSLR may be obstructed along the Atlantic coastline from extensive coastal development (e.g., Hopkinson et al., 2012).

### 4.1.2. Sedimentation Comparison Across Other Salt Marsh-Mangrove Ecotones

Our higher apparent sedimentation rates in transition and mangrove sites compared to salt marshes differed from studies in Louisiana, USA, showing equivalent sedimentation rates between mangroves and salt marshes (McKee & Vervaeke, 2018; Perry & Mendelssohn, 2009). In contrast, Comeaux et al. (2012) found that Texas mangroves had accumulation rates greater than salt marsh accumulation rates (3.1–8.2 mm yr$^{-1}$ vs. 1.7–3.6 mm yr$^{-1}$, respectively) and were contributed to a 4-cm greater elevation gain. Some argue age and spatial extent of mangrove stands likely explain sedimentation differences (e.g., mature mangroves in Texas versus young mangroves in Louisiana); however, our mangroves were young like those in Louisiana (mangrove stands cored in St. Augustine were not present in 2008) (Rodriguez et al., 2016) but had higher sedimentation rates in the mangrove and transition sites. This variability may relate to methodology, where the Louisiana studies used marker horizons, sediment traps, and $^{137}$Cs to estimate sedimentation rates, whereas this study and Comeaux et al. (2012) used $^{210}$Pb and $^{137}$Cs. These different methods utilize different timescales that could produce significantly different sedimentation rates, with marker horizons and $^{137}$Cs being more subdecadal and decadal versus $^{210}$Pb being more centennial (Breithaupt et al., 2018). Additionally, differences can be location specific (Breithaupt et al., 2018), where environmental factors like tidal range, groundwater flux, or warming could affect mangrove and salt marsh accretion. Warming of A. germinans and S. alterniflora plots in central Atlantic coast Florida wetlands resulted in significant elevation gains from greater root production in warmed mangrove plots than warmed salt marsh, unwarmed mangrove, and unwarmed salt marsh plots (Coldren et al., 2019). In contrast, freeze and wrack burial disturbances had no effect on elevation dynamics in Louisiana mangrove or salt marshes, though other physical factors like inorganic sedimentation, erosion, and auto-compaction could have influenced these dynamics (McKee & Vervaeke, 2018).

### 4.2. Transition Sites Burying More Carbon

The transition along both coasts had the highest %TOC and average carbon burial rates of the vegetation sites (Table 1), followed by the mangrove and salt marsh sites. This could be partially explained by biomass; however, mangrove sites had higher biomass with higher carbon concentrations yet produced the lowest %TOC. The mangroves also had lower average carbon burial rates compared to the transitions, suggesting that much of the biomass was lost. Generally, the wetland’s ability to trap particulate organic matter (POM), including biomass, is strongly linked to higher vegetation densities, heights, and rigidity.
(Fagherazzi et al., 2004; Nepf & Vivoni, 2000). Both mangrove sites had higher vegetation densities and heights today and likely in past mangrove expansions compared to the other sites; however, these mangrove sites were near the shorelines, located along the Matanzas River in St. Augustine and the Gulf of Mexico (GoM) in Waccasassa Bay. Autochthonous POM could thus been removed from the mangrove sites by wave erosion and tidal export compared to the more inland transition and salt marsh sites. This is not surprising, as much as 99% of litterfall carbon can be exported out of mangrove systems with tidal inundation (Adame & Lovelock, 2011; Saenger & Snedaker, 1993). POM lost from mangroves may have been deposited elsewhere across the different habitats of these wetland sites or exported to Matanzas River and/or the GoM. The mangrove sites also likely received the most mineral sediments of all three sites (Stumpf, 1983), which limits organic matter accumulation due to vertical accommodation space limitations (Morris et al., 2002; Rogers et al., 2019). The transition sites thus likely buried the most carbon from a combination of high vegetation density, producing and trapping more organic matter, and its more inland location, which likely reduced periods of tidal inundation. Reductions in tidal inundation could, in turn, reduce mineral sediment inputs, reduce tidal organic matter export, and increase potential contributions of organic matter to accommodation space.

Compared to global carbon burial averages, all sites from both coasts recorded lower average burial rates compared to mangroves and salt marshes globally (Table 1) (Mcleod et al., 2011). The mangrove and transition sites from both coasts do, however, have average carbon burial rates within the lower end of rates measured for mangroves along the Gulf Coast of south Florida (20–381 g C·m⁻²·yr⁻¹) (Cahoon & Lynch, 1997; Lynch, 1989), while both salt marsh carbon burial rates were lower than salt marshes surrounding the GoM (18–1,713 g C·m⁻²·yr⁻¹; includes Texas, Louisiana, Mississippi, and Florida) (Chmura et al., 2003). It is unclear whether belowground biomass, which could influence organic matter measurements, was removed in these other studies prior to determining organic matter content.

Our study adds to the growing number of studies looking at carbon burial differences between mangroves and salt marshes in areas experiencing mangrove expansions. Many North American studies focused on mangroves and salt marshes but not transition sites. These studies found similar or lower organic matter contents between salt marshes and mangroves in Louisiana (belowground biomass not separated) (Henry & Twilley, 2013) and Texas (live rooting removed) (Comeaux et al., 2012). However, another study using the same Texas cores showed significantly higher OC burial in mangroves compared to salt marshes (Bianchi et al., 2013), suggesting that these mangrove sites may have increased OC burial but not total organic matter. When comparing wetland sites in central Texas, Louisiana, and northern Florida (Cedar Key, ~25 km west of Waccasassa Bay), Yando et al. (2016) only found greater belowground productivity and soil carbon after mangrove expansion into salt marshes at the central Texas site. This was attributed to the drier climate and less productive succulent marsh vegetation in central Texas compared to Florida and Louisiana grasses. Differences in mangrove expansion effects on soil carbon between their Cedar Key site and our Waccasassa Bay site were not related to lower aboveground carbon production in Waccasassa Bay salt marshes as the Waccasassa Bay salt marsh had higher aboveground carbon production (42 kg C m⁻²) compared to Cedar Key (~0.24 kg C m⁻²) (Yando et al., 2016). Instead, such differences in mangrove expansion effects may relate to our Waccasassa Bay salt marsh site being a higher marsh habitat than their Cedar Key salt marsh based on their reported dominant vegetation (e.g., S. alterniflorus and B. maritima).

Other carbon burial studies looking at mangrove expansion effects globally have incorporated more transitional areas. For southeastern Australia, where mangroves have been expanding for ~70 yr, there were significant belowground carbon increases with mangroves that have been developing for at least 58 yr (unclear whether belowground biomass was separated). Younger mangroves did not have significantly different belowground carbon compared to salt marsh sites (Kelleway et al., 2016). A mangrove-marsh ecotone in South Africa showed similar results, with greater soil organic matter in mangroves (age unreported) relative to salt marshes (Geldenhuys et al., 2016). This study additionally found transition locations, where salt marsh and mangrove vegetation coexist, had higher soil organic matter compared to salt marshes, consistent with our findings.

In Merritt Island, Fl, south of our Atlantic coast study site, mangroves encroaching into salt marshes over a 7-yr period yielded insignificant differences in belowground biomass and soil for mangrove, salt marsh, and transitional sites despite greater aboveground biomass production in mangrove vegetation (Doughty...
et al., 2016). The young ages of the Merritt Island mangroves were used to explain the lack of differences. Both coasts in our study, however, had mangrove trees in the transitions that were patchy and likely younger given our more northern location, yet transitions still recorded significantly higher carbon stocks and higher average carbon burial rates. This suggests that other environmental variables besides mangrove stand ages could influence carbon burial more between locations.

4.3. Changes in Overall Carbon Quality Between Sites

Bulk isotopic and biomarker data helped evaluate how soil carbon pools differed between sites. Higher bulk C/N in transition sites indicate more terrestrial plant inputs, while lower C/N in mangrove sites could indicate more algal inputs (Meyers, 1994). High algal inputs within these mangroves were expected as both mangrove sites were close to shorelines, with algal material coming in and terrestrial litterfall exported out via wave/tidal action (Adame & Lovelock, 2011; Saenger & Snedaker, 1993). δ13C also followed expectations with the current St. Augustine low salt marsh, dominated by C4 S. alterniflorus and C3 B. maritima, and the current Waccasassa Bay transition, dominated by S. alterniflorus with other C3 grasses and mangroves, being more enriched than other sites.

Biomarkers evaluated how carbon sources and quality varied between more ubiquitous carbon pools (i.e., amino acids) versus those common to terrestrial vascular plants (i.e., lignin). The amino acid pools (based on THAA and AA N%) were significantly higher in Waccasassa Bay compared to St. Augustine, possibly reflective of higher aboveground biomass. Conversely, total lignin pools (Λ-6 and Λ-8) did not significantly differ between coasts, indicating that location and biomass likely did not affect soil lignin amounts.

Mangrove sites for both coasts had the highest amino acid concentrations, possibly reflecting higher algal and terrestrial material inputs. Lignin was conversely greatest in the St. Augustine salt marsh and transition and in the Waccasassa Bay transition. Algal material may have thus contributed more to the mangrove amino acid pools if there was overall more organic matter but less terrestrial vascular plant inputs. This supports possible wave/tidal export of vascular plant biomass from mangrove sites despite its high production. Higher Hyp concentrations, an amino acid found in terrestrial plants and green algae (Gotelli & Cleland, 1968; Voigt et al., 1994), in the mangrove sites may additionally indicate high algal inputs. Conversely, Hyp could indicate degradation as it is preferentially preserved during degradation (Philben et al., 2016; Philben & Benner, 2013). Of the terrestrial material that made it to the mangrove soils, C/V and S/V suggested that much of it came from woody angiosperm sources (e.g., mangroves) (Marchand et al., 2005). Unlike the mangroves, the transition sites likely received more terrestrial vascular plant inputs, as indicated by higher lignin content, due to the combination of high biomass and distance from the shoreline. C/V and S/V for soils in both transition sites indicated a mixture of woody (e.g., mangrove) and non-woody (e.g., salt marsh) angiosperm sources.

Soil OC degradation states differed between sites based on biomarker indices. The St. Augustine mangrove site had the lowest DI of all St. Augustine sites, indicating potentially higher amino acid degradation. Comparatively, lignin degradation indices, (Ad/Al), and (Ad/Al)o, were highest within the St. Augustine mangrove and transition and within the Waccasassa Bay mangrove and high salt marsh. This suggests that lignin in the mangrove sites was also degraded, likely by mixing sediment with wave/tidal energy combined with mangrove roots translocating oxygen to soils via gas exchange in aerial pneumatophores (Scholander et al., 1955; Andersen & Kristensen, 1988] and from mangrove crab bioturbation (Ferreira et al., 2007; Nielsen et al., 2003).

4.4. Changes in Carbon Downcore

Soil profiles represent a mixture of organic matter pools with components derived from varying sources and with varying degradation states. Additionally, physical processes (i.e., wave/tidal energy) and bioturbation could mix profiles, as demonstrated in the 210Pb (Figure S1), possibly diminishing any distinct changes with depth. Nonetheless, TOC decreased downcore for all sites and C/N increased downcore for most sites, typical of in situ diagenesis (e.g., Bianchi et al., 2013; Dittmar & Lara, 2001). Mangrove and transition sites for both coasts became 13C-enriched with depth, possibly from diagenetic processes discriminating against the 13C isotope and/or carbon source changes from more algal (δ13C of −16 to −28‰) (Fry & Sherr, 1989) or C4 terrestrial plant (e.g., S. alterniflorus) input. Given the dynamics of these mangrove-salt marsh ecotones (e.g., Rodriguez et al., 2016), these mangrove and transition sites could have previously had significant salt
marsh inputs. C/V, however, did not significantly change for most sites, indicating no significant shifts in woody versus nonwoody inputs. Conversely, higher C/V signals from nonwoody vegetation could be erased with the loss of cinnamyl over vanillyl phenols, with cinnamyls being more labile due to their ester-bound linkages (Bianchi et al., 2002; Hartley, 1973; Kirk et al., 1980).

The organic matter pools (i.e., amino acids and lignin) differed more downcore between coasts than the bulk OC isotope analyses. Decreases in amino acids for most profiles were expected from in situ diagenesis, similar to bulk OC. Conversely, lignin in most profiles was relatively uniform with depth, suggesting little degradation with depth or high lignin content inputs, possibly from previous mangrove expansions, that offset potential degradation.

The St. Augustine transition and low salt marsh did not have decreases in amino acids or stable lignin profiles. Both had some increase in amino acids at points within the profile and had general decreases in lignin with depth. Amino acid increases with depth do not imply a lack of diagenetic processes, as DI and Hyp increases downcore could suggest some amino acid degradation (Philben et al., 2016; Philben & Benner, 2013). It could also suggest that there were changes in amino acid amounts related to the dynamic mangrove migration. Shorter trees currently in the St. Augustine mangroves compared to Waccasassa Bay indicated that the St. Augustine mangroves were likely younger (e.g., Fromard et al., 1998) and may have recently migrated into the salt marsh. The transition from current mangrove to salt marsh vegetation in Waccasassa Bay was also more abrupt (i.e., shorter, more juvenile mangroves did not extend far into the salt marsh) compared to St. Augustine, possibly due to greater elevation change going from the shoreline to high marsh. Thus, changes in vegetation structure over a shorter time interval (going from salt marsh to mangrove) compared to St. Augustine, possibly due to greater elevation change going from the shoreline to high marsh. Thus, changes in vegetation structure over a shorter time interval (going from salt marsh to mangrove) compared to St. Augustine, possibly due to greater elevation change going from the shoreline to high marsh. Thus, changes in vegetation structure over a shorter time interval (going from salt marsh to mangrove) compared to St. Augustine, possibly due to greater elevation change going from the shoreline to high marsh. Thus, changes in vegetation structure over a shorter time interval (going from salt marsh to mangrove) compared to St. Augustine, possibly due to greater elevation change going from the shoreline to high marsh. Thus, changes in vegetation structure over a shorter time interval (going from salt marsh to mangrove) compared to St. Augustine, possibly due to greater elevation change going from the shoreline to high marsh. Thus, changes in vegetation structure over a shorter time interval (going from salt marsh to mangrove) compared to St. Augustine, possibly due to greater elevation change going from the shoreline to high marsh. Thus, changes in vegetation structure over a shorter time interval (going from salt marsh to mangrove) compared to St. Augustine, possibly due to greater elevation change going from the shoreline to high marsh.

4.5. Considerations for Future Salt Marsh-Mangrove Ecotone Studies

These results highlight that additional research is needed to address carbon burial changes related to mangrove encroachment into salt marshes. Here, we offer some possible improvements to better assess burial changes in these important habitats. First, replicate cores from each vegetation category (mangrove, salt marsh, and transition) would improve spatial variability and increase statistical confidence. Second, elevation measurements would help discern differences in sedimentation and carbon burial due to vegetation versus wetland location—as related to RSL and/or the tidal prism. Finally, future sedimentation or carbon burial work in these dynamic systems needs to consider using multiple methods spanning different timescales (e.g., 210Pb/137Cs, marker horizons, 14C) (e.g., Breithaupt et al., 2018); this will allow for better estimates of sedimentation and mixing rates over decadal, centennial, and millennial timescales.
5. Conclusions

St. Augustine and Waccasassa Bay Preserve State Park represented locations where mangroves are migrating into salt marshes due to increasing air temperatures and decreasing freeze event frequencies. Many prior studies suggested that this expansion did not increase sedimentation or carbon burial in tidal wetlands (e.g., Comeaux et al., 2012; Doughty et al., 2016; Henry & Twilley, 2013; Perry & Mendelsohn, 2009; Yando et al., 2016, 2018); however, our results, combined with results from Texas (Bianchi et al., 2013), demonstrate that there are sites with mangrove expansions that have increased sedimentation and carbon burial. Some of the sedimentation and burial increases may relate to the wetland’s ability to keep up with RSLR through mineral and organic sediment trapping (Morris et al., 2002; Rogers et al., 2019; Stumpf, 1983), though increased biomass production and more complex aboveground vegetation structures in mangrove sites could also increase OC inputs and increase the binding and trapping of sediments (Comeaux et al., 2012; Scoffin, 1970).

Shifts in vegetation amounts and type related to the mangrove expansion likely influenced the types of carbon preserved belowground. More ubiquitous carbon pools (e.g., amino acids) were related to aboveground biomass, with mangrove sites closer to the shorelines having higher algal contributions. The amino acids also seemed more susceptible to degradation as opposed to carbon pools considered more resistant to anaerobic degradation (e.g., lignin). Lignin, derived from terrestrial vascular plant inputs, did not link to aboveground biomass amounts, likely due to the export of vascular plant biomass with tidal and wave energy in shoreline mangrove systems. Additionally, lignin degradation belowground was likely influenced by oxygen availability, where sites with possibly greater physical mixing and deeper roots have enough oxygen to degrade lignin deeper in the soil than sites without mixing and deep roots.

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