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Carbon Storages along a Climate Induced Coastal Wetland Gradient

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Abstract Across the globe, coastal wetland vegetation distributions are changing in response to climate change. In the southeastern United States, increased winter temperatures have resulted in poleward range expansion of mangroves into pure salt marsh habitat. Climate change-induced expansion of mangroves into salt marsh will significantly alter carbon (C) storage capacity of these wetlands, which currently store the highest average C per land area among unmanaged terrestrial ecosystems. Total ecosystem C stocks were measured along a 342 km latitudinal gradient of mangrove – to – marsh dominance in Florida. Carbon stocks were quantified through measurements of above- and belowground biomass and soil C. Interior mangrove C stocks were greater than both salt marsh and ecotonal C stocks and soil C comprised the majority of each ecosystem C component (51–98%). The wetlands investigated in this study cover 38,532 ha, and store an average of 215 Mg of C ha^{-1}. Currently, mangroves cover 31% of the land area studied, storing 44% of the total C, whereas salt marshes occupy 68% of the wetland area and only store 55% of the C. Total conversion of salt marsh to mangrove may increase C storage by 26%, predominately due to increases in aboveground biomass.

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Introduction

Global climate change is driving the expansion of mangroves into salt marsh habitat around the world due to a myriad of reasons; including, but not limited to, increased atmospheric temperatures, increased flux of tidal nutrients, and disturbances that promote mangrove colonization (*e.g.*, Eslami-Andargoli et al. 2009; Doyle et al. 2010; Cavanaugh et al. 2014). In North America, the ecotonal boundary between mangroves and salt marshes is fluctuating in response to environmental conditions. Cold – sensitive mangroves die back during freeze events and expand during warm periods, creating a dynamic ecosystem (Stevens et al. 2006; Ross et al. 2000; Rodriguez et al. 2016; Osland et al. 2017). In fact, alterations in mangrove habitat distribution has been shown to expand and contract in Florida U.S.A. since 1942 (Rodriguez et al. 2016). For example, at the northernmost mangrove range limit in Florida, mangrove – dominated land area has doubled since 1984 (Cavanaugh et al. 2014) due to a decrease in freezing events. Changes of this magnitude in dominant plant cover have the potential to significantly alter habitat structure, function, and landscape C storage (McKee and Rooth 2008; Comeaux et al. 2012).

Alterations in habitat structure and function can have significant implications for regional and global C pools as mangrove and salt marsh habitats have been shown to sequester huge amounts of C relative to their spatial extent (Mcleod et al. 2011; Durate et al. 2005). Despite only comprising 0.7% of the world's tropical forest area (Giri et al. 2011), mangroves contain globally significant C pools, particularly in soils, storing up to three times more C per hectare than

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typical upland tropical forests (Donato et al. 2011; Kauffman et al. 2011). Vegetation in these coastal forest ecosystems is structurally and functionally distinct, with inherently different C storage capacity (Duarte et al., 2013; Alongi 2014) and C sequestration rates (Lovelock et al. 2014), indicating that conversion of the dominant vegetation cover will dramatically alter total C storage of a given area. For example, Doughty et al. (2016) found that newly established mangrove stands in Florida store twice as much total C and biomass as salt marsh and transitional vegetation classes, primarily due to differences in aboveground biomass. Furthermore, C storage capacity of temperate ecotonal mangroves may be substantially lower than tropical mangroves due to a reduction in mangrove height with latitude (Morrisey et al. 2010) and subsequent age of the stand (e.g. Lovelock et al. 2010). Total C storage per area of an ecotonal coastal wetland is likely dependent on structural characteristics within and among vegetation types, as well as fluctuations in the extent of each vegetation class.

In the present study, whole ecosystem C stocks of distinct coastal wetland vegetation classes were measured along a latitudinal gradient (Fig. 1) to better understand how a shift from salt marsh – to – mangrove habitat will affect C storage of these communities. As these ecosystems shift, plant productivity, biomass allocation and decomposition will be altered by both physical (e.g. temperature, precipitation, nutrients) and biological (e.g. species composition, plant competition) variables, ultimately affecting C storage of the system. Hence, the latitudinal transition from mangrove – to – salt marsh ecosystems along the Atlantic coast of Florida allows us to use a space for time substitution to determine how climate change will alter C stocks over time. The objectives of this study were to (1) quantify whole ecosystem organic C stocks of coastal wetlands along the Atlantic coast of Florida and (2) make inferences on the future C storage capacity of these dynamic ecosystems. We hypothesized that variability in total C stocks from one location to another will be a function of aboveground structure and soil C storage. Specifically, we hypothesized that ecotonal sites will store less C than pure mangrove sites, due to tree stature and density. Additionally, soil C will comprise a larger C reservoir than vegetative biomass. This study details the first whole-ecosystem C stock analysis of mangrove and salt marsh cover along the Atlantic coast of Florida, providing invaluable C stock baselines of these dynamic coastal habitats.

Methods

Study Sites

Ten sites, spanning 342 km along the east coast of Florida were selected for permanent plots (Fig. 1). Distances between study sites were approximately 37 km within the latitudes

26.8° N and 29.7° N. Sites were chosen based on minimal human disturbance (i.e., they were not previously impounded for mosquito control (e.g. Rey et al. 1991)) and geographic distance. Additionally, sites were not selected south of West Palm Beach (approximately 26°) due to sparse availability and heavy human disturbance. The spatial expanse of sampling sites allowed for quantification and comparison of ecosystem C stocks in four types of contrasting vegetation structures: (a) pure fringing mangroves, (b) pure interior mangroves, (c) ecotonal mangroves, and (d) pure salt marsh (Table 1).
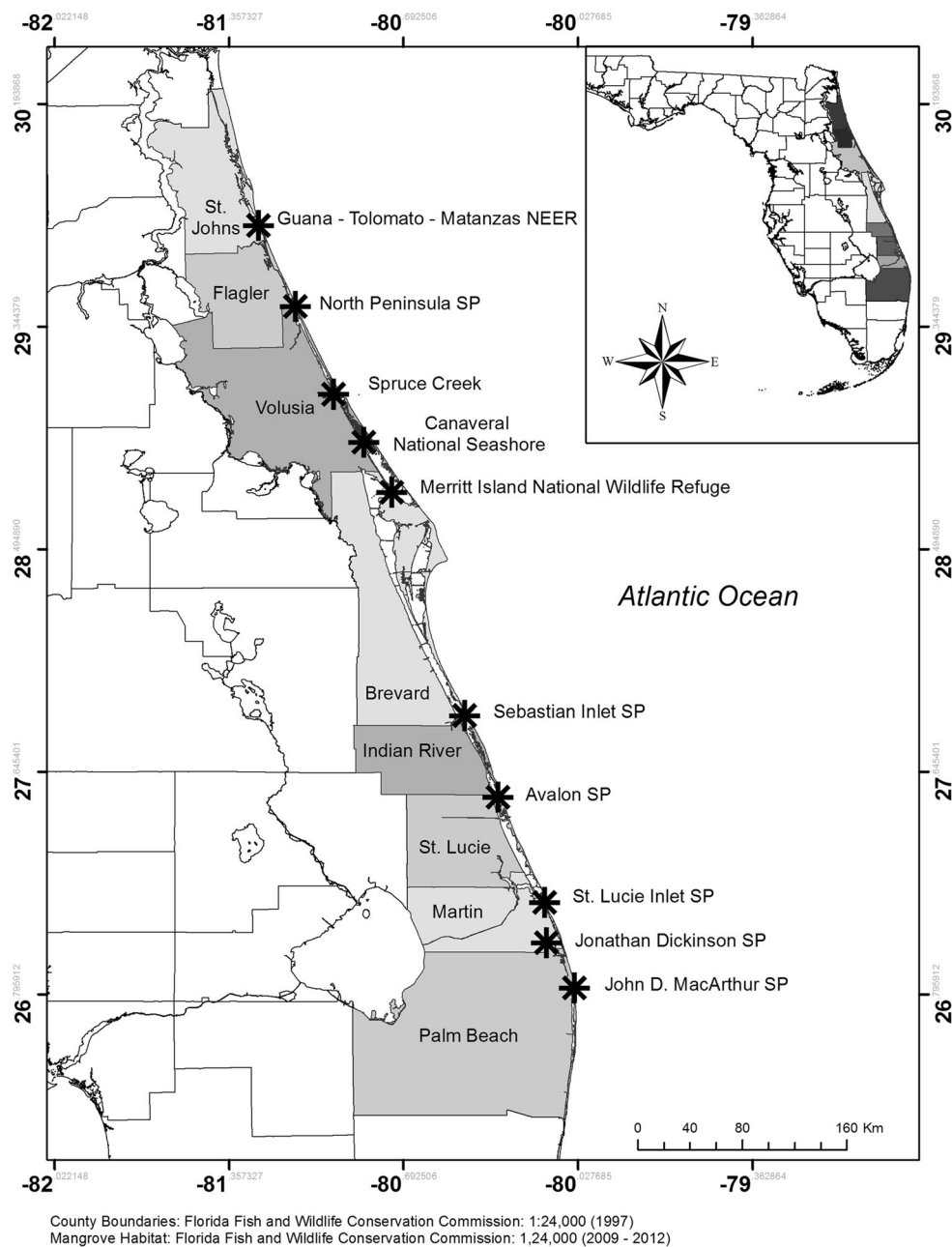
The southern sites (≤ 27° N Lat)(Sebastian Inlet State Park, Avalon State Park, St. Lucie Inlet State Park, Jonathan Dickinson State Park and John D. MacArthur State Park)(Fig. 1) were dominated by one to three species of medium-sized mangroves, including R. mangle, A. germinans, and Laguncularia racemosa (white mangrove). Trees found fringing the seaward edge were typically tall (~ 5 m), while those in the landward interior were shorter (~3 m) and denser in stature. Salt marsh species were absent from these sites. These sites had an average winter temperature of 21.9 ± 0.21 °C and an average summer temperature of 27.7 ± 1.06 °C.

The mangrove dominated sites of the south gave way to ecotonal and pure salt marsh stands in the north (≥ 28° N Lat) (Guana – Tolmato – Matanzas National Estuarine Research Reserve, North Peninsula State Park, Spruce Creek, Canaveral National Seashore and Merritt Island Wildlife Refuge) (Fig. 1). Ecotonal stands were comprised of a mixture of all three species of short-statured (dwarf) mangrove and salt marsh species. Pure salt marsh stands contained monocultures or polycultures of herbaceous or graminoid species. Salt marsh species included, but were not limited to, Spartina alterniflora (smooth cordgrass), Distichlis spicata (saltgrass), Salicornia bigelovii (annual glasswort), Salicornia virginica (Virginia glasswort), Batis maritima (saltwort) and Sueda linearis (sea blite). These sites had an average winter temperature of 21.9 ± 0.20 °C and average summer temperature of 30.0 ± 0.14 °C.

Field Sampling

Within each of the ten sites, 10 × 10 m permanent plots were established in the fringe and interior. Fringe plots were established 10 m from the seaward edge and ≤10 m from one another. Interior plots were established approximately 30–80 m landward of the fringe plots (Fig 2b). The five northern sites had six plots per site, three plots in the fringe (ecotone), and three within the interior (salt marsh). In the five southern sites, there were three sites with six plots (three plots in the fringe (mangrove) and three plots in the interior (mangrove)), while two of the sites only had three plots in the fringe. In total, 54 plots were sampled across the ten sites (Fig. 2a). Nested 1 m² subplots (n = 3) were established within

Fig. 1 Site locations of permanent plots along the Atlantic coast of Florida. County names are provided in areas studied and asterisks denote parks in which sites were located

County Boundaries: Florida Fish and Wildlife Conservation Commission: 1:24,000 (1997)
Mangrove Habitat: Florida Fish and Wildlife Conservation Commission: 1,24,000 (2009 - 2012)

each 100 m^2 plot for measurements that required smaller areas (*i.e.,* seedling and pneumatophore counts) (Fig 2c).

At each plot, necessary data was collected to calculate total C stocks derived from standing biomass, downed wood and soil to 50 cm following methodologies outlined by Kauffman and Donato (2012). Samples were collected for each C pool at one time point during the study period (July 2013 – October 2015). Herbaceous species biomass in temperate regions slows during winter months (Pennings and Bertness, 2001), so biomass was collected in July 2015 to capture the height of C sequestration.

Aboveground Biomass

To quantify the size of the aboveground biomass C pool in these ecosystems, mangrove and salt marsh biomass, species density data, and downed wood biomass measurements were collected. Species composition, tree density and basal diameter were quantified through measurements on all trees rooted within a 5 × 5 m quadrat of the 10 × 10 m plot.

Diameter at breast height (DBH) measurements were taken on all trees to calculate biomass through species-specific allometric equations. Allometric equations often show site- or species dependency (*e.g.* Clough et al. 1997; Smith and

Table 1 Characteristics of sampling locations

Site	Plot	Latitude/Longitude	Canopy Height (m)	Density (tree ha⁻¹)	Dominant mangrove	Dominant salt marsh
Guana Tolomato Matanzas NEER	Fringe	N 29.72°	0.83 ± 0.2	13,733.33 ± 6367.13	Avi (100%)	Bat (61%)
		W − 81.24°				Sal (48%)
	Interior	N 29.73°				Spr (80%)
		W − 81.25°				Bat (10%)
North Peninsula SP	Fringe	N 29.41°	0.97 ± 0.3	25,866.67 ± 7528.96	Avi (100%)	Bat (5%)
		W − 81.10°				Sal (4%)
	Interior	N 29.42°				Spr (58%)
		W − 81.10°				Dis (42%)
Spruce Creek	Fringe	N 29.08°	1.11 ± 0.6	20,266.67 ± 5319.59	Avi (74%)	Bat (13%)
		W − 80.95°			Lag (15%)	Sal (5%)
	Interior	N 29.08°				Spr (58%)
		W − 80.96°				Sal (10%)
Canaveral National Seashore	Fringe	N 28.90°	0.83 ± 0.2	22,800.00 ± 10,165.-53	Avi (100%)	Bat (7%)
		W − 80.84°				Sal (7%)
	Interior	N 28.90°				Dis (99%)
		W − 80.84°				Bat (1%)
Merritt Island NWR	Fringe	N 28.70°	0.84 ± 0.1	29,066.67 ± 6312.32	Lag (87%)	Bat (9%)
		W − 80.73°			Avi (13%)	Sal (36%)
	Interior	N 28.71°				Dis (100%)
		W − 80.74°				
Sebastian Inlet SP	Fringe	N 27.85°	3.07 ± 0.1	18,933.33 ± 1140.55	Rhiz (92%)	-
		W − 80.45°			Lag (8%)	
	Interior	N 27.86°	2.99 ± 0.12	20,266.67 ± 4340.01	Rhiz (100%)	-
		W − 80.46°				
Avalon SP	Fringe	N 27.54°	3.64 ± 0.17	12,533.33 ± 2245.67	Rhiz (93%)	-
		W − 80.33°			Avi (6%)	
	Interior	-	-			-
St. Lucie Inlet SP	Fringe	N 27.14°	5.11 ± 0.12	5300.00 ± 529.77	Rhiz (96%)	Lag (4%)
		W − 80.15°				
	Interior	N 27.14°	2.06 ± 0.1	8866.67 ± 318.35	Rhiz (84%)	-
		W − 80.15°				
Jonathan Dickenson SP	Fringe	N 26.98°	6.45 ± 0.2	11,600.00 ± 1443.93	Rhiz (100%)	-
		W − 80.14°				
	Interior	N 26.99°	4.89 ± 0.16	16,000.00 ± 6011.56	Rhiz (96%)	-
		W − 80.15°			Lag (4%)	
John D. MacArthur SP	Fringe	N 26.81°	4.58 ± 0.3	5066.67 ± 533.96	Rhiz (86%)	-
		W − 80.04°			Avi (13%)	
	Interior	-	-	-		-

Values are shown as mean ± SE. Avi = *Avicennia germinans*, Lag = *Laguncularia racemosa*, Rhiz = *Rhizophora mangle*, Bat = *Batis maritime*, Sal = *Salcornia bigloveii*, Spr = *Spartina alterniflora*, Dis = *Disticulus spicata*. SP = State Park. In the top five sites, fringe = ecotonal plot, interior = pure salt marsh plot. In the bottom five sites, fringe and interior = pure mangrove

Whelan 2006); hence, DBH measurements and allometric equations used were specific to Florida mangroves (Table 2). Additionally, the allometric equation used for dwarf *A. germinans* was formulated specifically for this study. Ten trees from the Guana – Tolomata – Matanzas National Estuarine Research Reserve in St. Augustine, FL were selected for allometric equation development. The height, crown diameter and basal diameter at multiple points were measured for each individual. Once *in situ* measurements were recorded, each individual was cut and transported back to the lab for processing. We developed and compared multiple allometric equations using various combinations of

Fig. 2 (a) Ten sites were studied along a 342 km gradient. Each symbol represents a site that had plots in the (b) fringe and in the interior. Asterisks represent sites where fringe plots were comprised of mangrove – salt marsh ecotone, and interior plots were pure salt marsh. Stars represent sites where fringe and interior plots were both pure mangrove stands. (c) Each plot measured 100 m^2 and was quartered off into 25 m^2 sections. In addition, three 1 m^2 quadrats (white boxes) were roped off per plot to allow for subsampling of undisturbed areas within the plots. In total, 54 plots were sampled
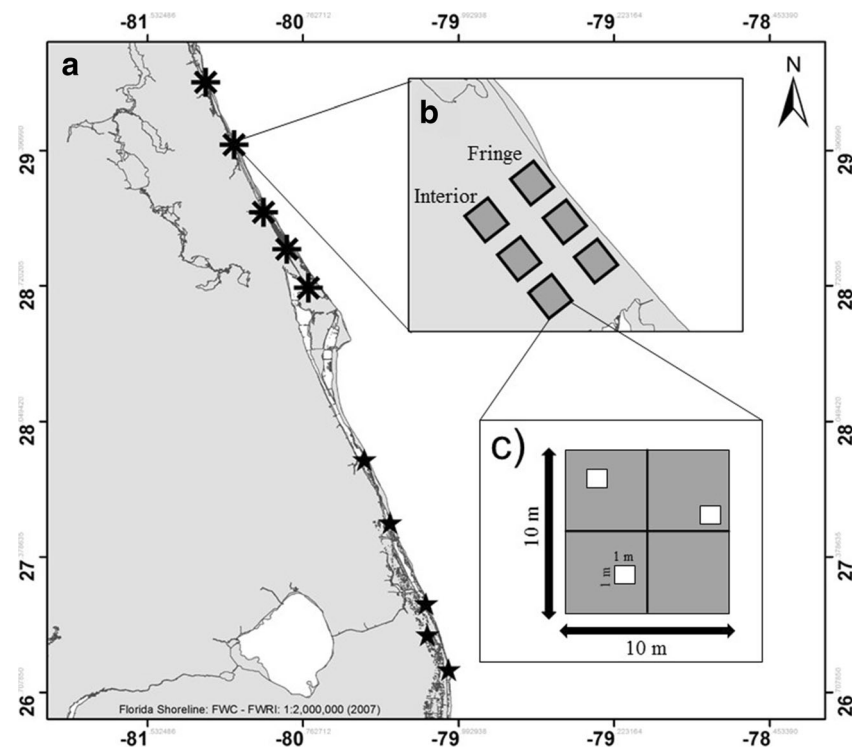
predictor and response variables resulting in the selection of the equation that uses the DBH taken just above the soil surface (Table 2). Biomass measurements were then multiplied by a factor of 0.48 to calculate standing tree C stock (Kauffman and Donato 2012).

Pneumatophore biomass of *A. germinans* was calculated independently because they are not historically included in published allometric equations. Pneumatophores were destructively sampled in one 1 m^2 subplot of each 10 × 10 m plot. All pneumatophores were cut at ground level, counted and dried to a constant weight. Pneumatophore biomass were calculated as the dry mass of sampled pneumatophores divided by the number of pneumatophores in each subplot. A

conversion factor of 0.39 (Kauffman and Donato 2012) was used to obtain pneumatophore C content. Litter was also sampled in all 1 m^2 subplots. All organic surface material, excluding woody particles, was collected, and dried at 70 °C in the lab until a constant weight was reached. A conversion factor of 0.45 (Kauffman and Donato 2012) was used to obtain mean C concentration.

Downed wood (CWD) was sampled in a 5 × 5 m quadrat per 10 × 10 m plot, using a protocol adopted from Feller and others (2015). All dead wood (both on the ground and in the canopy) were removed, weighed, and categorized by size. Categories consisted of small wood debris, > 2.5 cm but <7.5 cm in diameter, and

Table 2 Aboveground allometric equations for mature tall and dwarf mangroves

Species	Aboveground Biomass Allometric Equation	Reference
R. mangle (tall)	$\log_{10} B = 1.731 * \log_{10} D_R - 0.112$	Smith and Whelan (2006)
R. mangle (dwarf)	Ln B (g) = $2.528 + (1.129 \, (\text{Ln } D_5^2 \, (cm)) + (0.156 * \text{Ln Crown Volume (cm}^3))$	Ross et al. (2001)
A. germinans (tall)	$\log_{10} B \, (kg) = 1.934 * \log_{10} DBH \, (cm) - 0.395$	Smith and Whelan (2006)
A. germinans (dwarf)	$\text{Log}_{10} B (g) = 2.19 \, \text{Log}_{10} (DBH) - 3.39$	This study
L. racesmosa (general)	$\log_{10} B \, (kg) = 1.930 * \log_{10} DBH \, (cm) - 0.441$	Smith and Whelan (2006)

DBH for *R. mangle* (tall and dwarf) was measured directly above the highest buttressing prop root. DBH on tall *A. germinans* and *L. racemosa* was measured 1.4 m above the soil surface. DBH on dwarf *A. germinans* was measured just above the soil surface

large wood debris, > 7.5 cm. Large downed wood was separated into two classes; sound and partially decomposed. Wood debris was considered partially decomposed if it visually appeared rotten and broke apart when handled. A subsample was oven-dried to determine a conversion factor for estimating dry weight per sample, which was then used for estimating biomass of the woody debris (g m^{-2}). Components of woody debris could not be identified conclusively to species and prevented use of species specific densities. A conversion factor of 0.45 (Kauffman and Donato 2012) was used to obtain mean C concentration.

Aboveground biomass estimates for salt marsh species were determined via destructive harvesting of one 1 m^2 subplot in each 10 × 10 m plot. Aboveground shoots were dried at 60 °C until a constant weight, massed and ground in preparation for C:N analysis. Percent C was multiplied by biomass to estimate total aboveground C in salt marsh vegetation. Values used were as follows: *B. martima,* 0.32; *S. virginica,* 0.32; *S. alterniflora,* 0.45; *D. spicata,* 0.45.

Belowground Biomass

Root biomass for mangrove trees was calculated using the general formula by Komiyama and others (2008): $B_{TB} = 0.199*\rho^{0.899}*(D)^{2.22}$, where B_{TB} = Tree belowground biomass (kg), ρ = wood density (g cm^{-3}), D = tree diameter at breast height (cm). Wood density values used were as follows: *R. mangle,* 0.83; *A. germinans,* 0.66; and *L. racemosa,* 0.60 (Kauffman and Donato 2012). A conversion factor of 0.39 was used to calculate belowground biomass C, as recommended by Kauffman and Donato (2012).

Soil cores (20 cm in length and 5 cm in diameter) were taken to estimate salt marsh belowground biomass. Roots were separated from soil by washing the 20 cm core in a 2 mm sieve. Flow-through matter was collected by a 0.5 mm sieve and placed in water to separate sediment from live fine roots. Large mangrove roots were removed from the samples. Roots were dried at 60 °C until a constant weight and weighed to determine belowground biomass to a depth of 20 cm. The C conversion factor of 0.34 (Duarte 1999) was used to obtain belowground C stores.

Soil Carbon

At each plot, a 50 cm core was collected using a 10 cm inner diameter stainless steel corer. The cores were systematically divided in the field into 5 cm increments. At some sites, a depth of 50 cm was not attainable due to a shallow sand layer, so the best possible core was taken. A maximum depth of 50 cm was used to ensure uniformity of samples, but likely underestimates soil C stocks because of C storage at deeper depths. Soil depths to refusal were not taken at each plot due to

the wide variability of sites. Core samples were kept cool and out of direct sunlight prior to being returned to the laboratory for analysis. A compaction correction factor was used in instances when compaction was unavoidable (Howard et al. 2014). In the lab, soil samples were stored at 4 °C prior to analysis, then dried at 70 °C until they reached a constant weight. Subsamples of a known volume were dried to a constant mass to determine bulk density (BD). BD (g cm^{-3}) of each sample was calculated by dividing the oven dried mass by the volume of the sample. Samples were ball milled with a Mixer/Mill 8000D (SPEX, Metuchen, New Jersey, U.S.A.) to ensure homogeneity prior to analysis for total C (TC), total N (TN), loss on ignition (LOI) and organic C (OC) measurements. Subsamples of the homogenized soils were combusted using a CE – 440 elemental analyzer (Exeter Analytical, Inc. Chelmsford, Massachusetts, U.S.A.) for TC and TN. Remaining subsamples were combusted at 500 °C for 4 h in a Lindberg/Blue MTM MoldathermTM box furnace (Thermo Fischer Scientific, Waltham, Massachusetts, U.S.A) for LOI measurements. OC pools were obtained as the product of total soil C (TC) and bulk density to 50 cm. Total soil C per sampled depth interval was calculated for each core then summed and scaled up to determine total soil C (Mg C ha^{-1}) at each sampling location.

Total Ecosystem C Stock

Total ecosystem C stocks were defined as the sum of total C in vegetation, downed wood, and soils to 50 cm. Total ecosystem C stocks (Mg C ha^{-1}) for each vegetation type were estimated by summing the C stock values for each of the component pools: Ecosystem C = $C_{above} + C_{below} + C_{litter} + C_{cwd} + C_{pneu} + C_{soil}$, where each term is the C stock (Mg C ha^{-1}) for each compartment. C_{above} describes aboveground biomass, C_{below} describes belowground biomass, C_{litter} describes leaf litter, C_{cwd} describes downed wood, C_{pneu} describes pneumatophores, and C_{soil} describes soils to 50 cm. Mangrove and salt marsh stock estimates were summed for the ecotonal category.

To scale up ecosystem C stocks from West Palm Beach to St. Augustine, mangrove and salt marsh land cover maps of Florida for 2009–2012 were obtained through the Florida Fish and Wildlife Conservation Commission (FWC 2009). The land cover shapefiles encompass the entirely of the state and the mangrove shapefile does not take into account differences in mangrove structure (*i.e.* dwarf, interior). Because we were only interested in the 342 km gradient studied, and as to prevent scaling discrepancies related to variation in vegetation types across latitudes, mangrove and salt marsh cover shapefiles were limited (by clipping) to counties where study sites were present. Counties that did not have a site in them were discarded and eight remaining counties were investigated (Palm Beach, Martin, St. Lucie, Indian River, Brevard,

Volusia, Flagler and St. Johns) (Fig. 1). Mangrove and salt marsh area of the eight counties were then calculated and multiplied by total C stock estimates of corresponding sites studied to obtain a baseline calculation of C stocks (Mg C ha^{-1}) along the Atlantic coast of Florida. Because biomass varies along the gradient, and different allometric equations were used based on mangrove structure, sites corresponding to the counties they are found in will likely decrease variability in C stock estimates. Analysis of species area was done in ArcGIS 10.4.1 (Esri, Redlands, California, U.S.A).

Environmental Characteristics

Environmental characteristics were collected in each plot to capture any spatial or temporal differences along the latitudinal gradient. Porewater was extracted from the ground at 15 cm using a sipper (McKee et al. 1988) and salinity was measured with a refractometer every 3 months. Atmospheric temperature was recorded from January 2015 – January 2016 with HOBO pendant temperature loggers (Onset Computer Corporation, Bourne, Massachusetts, U.S.A.). pH was measured in the field at 3 month intervals with an IQ 150 (Spectrum technologies, Inc., Aurora, Illinois, U.S.A.).

Statistical Analysis

A one – way analysis of variance (ANOVA) was used to determine potential differences among biomass components (aboveground, belowground, pneumatophores, litter, and CWD) and C stocks across vegetation types (fringe, interior, ecotonal, salt marsh) where vegetation type was the fixed effect and site (nested in vegetation type) was the random effect of the model. Differences in soil properties (BD, LOI, TC, TN, and OC) across vegetation types were also tested with ANOVA, with vegetation type as the fixed factor and site as the random effect of the model. Differences in soil BD, LOI, TC, TN, and OC by depth were also tested with ANOVA, with depth as the fixed factor and site as the random effect of the model. A two – way ANOVA was used to test for interactions between vegetation type and season on temperature. Normality was assessed using the Shapiro – Wilks test and homogeneity of samples was assessed using Levene's test. When required, variables were log transformed to comply with normality and homogeneity of variances when testing linear models. When significant differences were found, pair-wise comparisons were explored with Tukey's honestly significant differences test. α was set at 0.05. Linear regression correlations between soil properties (BD and TC, LOI and TC, soil C and soil N) were analyzed using samples across all sites and all depth horizons. Multiple regressions were used to test the effect BD and LOI on C stocks. Analyses were performed using JMP 5.0. (S.A.S Inc., Cary, North Carolina,

U.S.A.). Throughout the manuscript, data are reported as mean ± standard error.

Results

Vegetation Composition

Coastal wetlands along the Atlantic coast of Florida were composed of at least four distinct vegetation types (Table 1). In the southern range of the state (26 °N – 27 °N), tall *R. mangle* (with a mean height of 5.03 ± 0.08 m) comprised 93% of the fringe plots. Interior plots, those found farther back in the intertidal, were comprised mainly of *R. mangle* (93%) and had an average height of 3.39 ± 0.07 m. Mangrove biomass density was significantly different between all southern fringe and interior plots ($F_{1,22} = 4.57$, $p = 0.05$), as suggested by Woodroffe (1992). Interior mangroves had a density of 15,044 ± 3556 trees ha^{-1}, whereas fringing mangroves had an average density of 10,686 ± 1178 trees ha^{-1}. In the northern range of the state (28 °N - 29 °N), tall *R. mangle* gave way to dwarf *A. germinans* (77.4%), which averaged 0.92 m ± 0.01 m in height and had an average density of 22,346 ± 7138 trees ha^{-1}. Dominant herbaceous species were *S. bigelovii* and *B. maritima*. Finally, interior salt marsh plots contained either monocultures or assemblages of *S. alterniflora*, *D. spicata*, *S. bigelovii*, *S. virginica*, and *B. maritima* (Table 1).

Biomass Stocks

Total tree biomass of coastal wetlands ranged from 102. ± 16.5 Mg ha^{-1} in ecotonal mangroves to 291. ± 21.6 Mg ha^{-1} in interior mangroves. Above- and belowground biomass (Mg ha^{-1}) and total biomass C stocks (Mg C ha^{-1}) of interior mangroves were significantly greater than ecotonal mangroves and salt marsh biomass ($F_{3,50} = 34.9$, $p \leq 0.0001$, $F_{2,36} = 9.02$, $p = 0.0007$, respectively) (Fig. 3). Total above- and belowground biomass stocks decreased with an increase in latitude ($F_{3,50} = 13.2$, $p \leq 0.0001$, $F_{3,50} = 17.1$, $p \leq 0.0001$, respectively) (Table 3). There was significantly more pneumatophore biomass and C (Mg C ha^{-1}) in ecotonal sites, than in mangrove and salt marsh sites ($F_{3,50} = 21.7$, $p \leq 0.0001$), due to the greater percentage of *A. germinans* in northern sites. Variations in litter were not significantly different across ecotypes ($F_{3,50} = 2.09$, $p = 0.11$).

Contributions of CWD to ecosystem C stocks were minimal, ranging from 1.12 ± 0.1 Mg C ha^{-1} in fringing mangroves to 0.20 ± 0.05 Mg C ha^{-1} in ecotonal mangroves; CWD varied significantly in the fringing/interior plots when compared to ecotonal/salt marsh plots ($F_{3,50} = 33.6$,
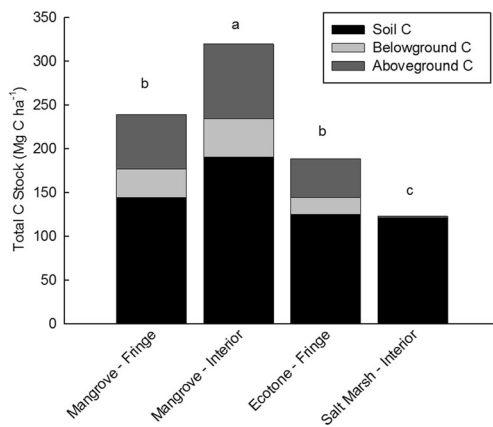
Fig. 3 Total ecosystem C stocks. Carbon stocks vary significantly across habitat types ($F_{3,50} = 15.8$, $p \leq 0.0001$). Different letters denote significantly different groups. Ecotone stocks are composed of both mangrove and salt marsh measurements. Values are means. Standard error bars were left off graph for visual simplicity

$p \leq 0.0001$). There was significantly more CWD in southern latitudes than in northern ($F_{3,50} = 28.9$, $p \leq 0.0001$) (Table 3). At the time of collection, CWD present was primarily in the sound-wood decay class, and the decomposed-wood class was negligible. Small wood and twigs contributed to 95% to the downed wood C stock, while large sound wood contributed 5%. Large rotten wood had zero contribution.

Soil Carbon Stocks

Bulk density was significantly different across depths ($F_{9,407} = 3.57$, $p = 0.0003$), ranging from 0.64 ± 0.06 g cm^3 in the upper 0–25 cm to 0.79 ± 0.08 g cm^3 in 25–50 cm. However, it was not significantly different across vegetation types ($F_{3,50} = 1.63$, $p = 0.19$) (Table 4). Soil OC (%) varied significantly across soil depths. As depth increased, soil OC (%) decreased ($F_{9,407} = 1.85$, $p = 0.05$), but was not significantly different across vegetation types ($F_{3,50} = 0.76$, $p = 0.52$) (Table 4). Organic matter content (LOI) (%) was not significantly different across soil depths ($F_{9,407} = 1.67$, $p = 0.09$) or

vegetation types ($F_{3,50} = 0.97$, $p = 0.42$) (Table 4). Mean soil TC (Mg C ha^{-1}) was significantly different between interior mangroves and all other vegetation types (Table 4). Soil C was significantly different across soil profile depth ($F_{9,407} = 3.45$, $p = 0.004$), ranging from 22.4 ± 1.29 Mg C ha^{-1} in the upper 5 cm section of the soil profile to 12.3 ± 2.29 Mg C ha^{-1} in the 45–50 cm section. Soil C was not significantly different across latitudes ($p = 0.08$). Total N (Mg N ha^{-1}) was not significantly different across vegetation types ($p = 0.79$) however, it was significantly different across depths ($F_{9,407} = 4.21$, $p \leq 0.0001$) (Table 4). Total N was highest in the shallow layers and decreased with depth, ranging from 1.43 ± 0.86 Mg N ha^{-1} to 0.66 ± 0.15 Mg N ha^{-1}.

Total Ecosystem Carbon Stocks

Mean ecosystem C stocks varied significantly across vegetation types: interior mangroves (320 ± 22.1 Mg C ha^{-1}), fringing mangroves (241 ± 30.6 Mg C ha^{-1}), ecotonal habitat (189 ± 23.2 Mg C ha^{-1}) and salt marsh (123 ± 5.03 Mg C ha^{-1}) ($F_{3,50} = 15.8$, $p \leq 0.0001$) (Fig. 3). Interior mangrove C stocks were 2.6 times greater than salt marsh C stocks and 1.7 times greater than ecotonal C stocks. Total C stocks were significantly different across latitudes. There was a 42% decrease in total C stock with an increase in latitude from 26 °N to 29 °N ($F_{3,50} = 9.23$, $p \leq 0.0001$) (Table 3).

When mangrove vegetation classes are aggregated, there are 12,106 ha of mangroves and 26,436 ha of salt marsh, for a total of 38,542 ha of coastal wetlands found in the eight counties studied. By scaling up, we estimate that the coastal wetlands along the 342 km swath studied on the Atlantic coast of Florida store 307 Mg mangrove C ha^{-1} and 173 Mg salt marsh C ha^{-1}, for a total of 8,290,005 Mg C. On average, there is 215.15 Mg C ha^{-1} within the area studied. Currently, mangroves cover 31% of the land area and store 44% of the total C, whereas salt marsh occupies 68% of the wetland area and only stores 55% of the C in these coastal ecosystems.

Table 3 Carbon stock compartments (Mg C ha^{-1}) across latitudes and vegetation types

LATITUDE	PLOT	AGB	BGB	CWD	PNE	SOIL
29°	Fringe	37.2 ± 9.08	14.3 ± 3.40	0.03 ± 0.02	0.61 ± 0.12	$121. \pm 18.5$
	Interior	2.46 ± 0.35	0.00 ± 0.0*	0.00 ± 0.00	0.00 ± 0.00	$112. \pm 30.1$
28°	Fringe	51.1 ± 9.25	27.0 ± 7.10	0.01 ± 0.01	0.67 ± 0.08	$131. \pm 17.2$
	Interior	1.86 ± 0.22	0.00 ± 0.0*	0.00 ± 0.00	0.00 ± 0.00	$133. \pm 9.77$
27°	Fringe	61.2 ± 8.65	29.3 ± 5.32	1.26 ± 0.15	0.32 ± 0.07	$131. \pm 13.0$
	Interior	80.9 ± 6.01	41.2 ± 3.81	0.80 ± 0.29	0.27 ± 0.05	$152. \pm 19.6$
26°	Fringe	65.4 ± 13.6	38.4 ± 7.76	0.93 ± 0.21	0.07 ± 0.02	$163. \pm 43.9$
	Interior	93.2 ± 16.9	51.2 ± 5.54	0.29 ± 0.08	0.07 ± 0.03	$226. \pm 24.5$

Values shown are mean ± SE (Mg C ha^{-1}). AGB: Aboveground biomass, BGB: belowground biomass, CWD: coarse woody debris, PNE: pneumataphores. *Numbers are too small to document. 29° – 28°: fringe = ecotonal plot, interior = pure salt marsh plot. 27° – 26°: fringe and interior = pure mangrove

Table 4 Soil summary values down the soil profile

Soil Depth (cm)	Bulk Density (g cm^{-3})	OC (%)	LOI (%)	Soil TC (Mg C ha^{-1})	Soil TN (Mg N ha^{-1})
Fringe					
0–5	0.63 ± 0.09	12.2 ± 1.63	22.4 ± 3.93	25.9 ± 3.31	1.43 ± 0.16
5–10	0.68 ± 0.09	11.7 ± 1.93	21.3 ± 4.66	17.1 ± 2.20	1.33 ± 0.13
10–15	0.70 ± 0.08	11.1 ± 2.17	19.8 ± 5.23	20.1 ± 1.69	1.67 ± 0.08
15–20	0.75 ± 0.08	10.4 ± 2.10	18.0 ± 5.16	16.7 ± 1.68	0.92 ± 0.09
20–25	0.80 ± 0.09	9.84 ± 2.09	16.8 ± 5.05	18.3 ± 1.91	0.92 ± 0.09
25–30	0.84 ± 0.13	11.6 ± 2.57	21.1 ± 6.18	14.4 ± 3.48	0.67 ± 0.17
30–35	0.67 ± 0.14	16.2 ± 3.13	32.0 ± 7.54	7.65 ± 2.83	0.43 ± 0.17
35–40	0.65 ± 0.16	17.7 ± 3.20	35.7 ± 7.71	7.16 ± 3.00	0.37 ± 0.17
40–45	0.50 ± 0.13	18.6 ± 3.22	37.8 ± 7.77	4.66 ± 2.58	0.24 ± 0.14
45–50	0.21 ± 0.03	24.4 ± 1.78	51.8 ± 4.29	3.06 ± 2.12	0.19 ± 0.13
Interior					
0–5	0.48 ± 0.09	17.1 ± 3.54	34.2 ± 8.54	17.1 ± 4.07	0.91 ± 0.21
5–10	0.67 ± 0.13	15.1 ± 4.30	29.5 ± 10.4	14.7 ± 4.95	0.74 ± 0.25
10–15	0.75 ± 0.15	14.5 ± 4.58	27.8 ± 11.0	15.4 ± 5.29	0.71 ± 0.28
15–20	0.78 ± 0.16	14.7 ± 4.7	28.4 ± 11.3	15.5 ± 5.75	0.79 ± 0.33
20–25	0.82 ± 0.18	14.8 ± 4.8	28.8 ± 11.6	14.8 ± 5.63	0.75 ± 0.32
25–30	0.80 ± 0.17	17.2 ± 4.9	34.5 ± 11.8	15.6 ± 5.78	0.79 ± 0.35
30–35	0.83 ± 0.21	17.8 ± 5.51	36.0 ± 17.8	19.0 ± 6.36	0.99 ± 0.40
35–40	0.45 ± 0.19	27.0 ± 5.10	58.1 ± 12.3	29.3 ± 5.91	1.62 ± 0.37
40–45	0.17 ± 0.01	32.7 ± 0.49	71.8 ± 1.18	35.67 ± 1.28	2.12 ± 0.13
45–50	-	-	-	-	-
Ecotonal					
0–5	0.46 ± 0.83	14.8 ± 2.08	28.6 ± 5.00	20.5 ± 1.73	1.50 ± 0.11
5–10	0.46 ± 0.09	16.2 ± 2.51	32.0 ± 6.05	17.8 ± 1.67	1.35 ± 0.12
10–15	0.56 ± 0.11	12.9 ± 1.93	24.2 ± 4.65	16.2 ± 2.43	1.13 ± 0.16
15–20	0.67 ± 0.12	11.5 ± 1.68	20.7 ± 4.04	16.8 ± 2.80	1.23 ± 0.22
20–25	0.87 ± 0.11	9.23 ± 1.39	15.3 ± 3.34	12.5 ± 1.99	0.82 ± 0.14
25–30	0.95 ± 0.12	8.63 ± 1.50	13.9 ± 3.62	12.1 ± 2.24	0.88 ± 0.16
30–35	1.06 ± 0.12	6.81 ± 1.05	9.54 ± 2.54	11.1 ± 1.92	1.19 ± 0.38
35–40	0.92 ± 0.12	7.00 ± 1.05	9.90 ± 2.54	7.04 ± 2.10	0.49 ± 0.14
40–45	0.98 ± 0.08	6.81 ± 0.84	9.43 ± 2.03	6.96 ± 1.99	0.46 ± 0.13
45–50	1.00 ± 0.08	6.61 ± 0.86	8.98 ± 2.09	3.91 ± 1.72	0.22 ± 0.10
Salt Marsh					
0–5	0.46 ± 0.11	18.9 ± 2.88	38.6 ± 6.95	17.7 ± 2.32	1.33 ± 0.18
5–10	0.50 ± 0.14	18.3 ± 2.63	37.1 ± 6.35	16.37 ± 2.30	1.14 ± 0.17
10–15	0.48 ± 0.12	16.8 ± 2.20	33.5 ± 5.31	16.0 ± 2.70	1.12 ± 0.19
15–20	0.62 ± 0.13	13.5 ± 1.93	25.5 ± 4.67	17.9 ± 3.57	1.16 ± 0.23

Values shown are mean ± SE. OC (%) = organic carbon. LOI (%) = loss on ignition. TC = total carbon. TN = total nitrogen

Environmental Characteristics

Interstitial salinity ranged widely across plots, depending on the season. In summer months (June – September), salinity averaged 37.6 ± 2.15 ‰ while in winter months (December – February) salinity decreased to 29.9 ± 1.08 ‰. In general, salinity values were lowest in interior and fringing mangrove plots (25.0 ± 1.43 ‰ and 29.0 ± 1.44 ‰, respectively) and highest in ecotonal and salt marsh plots (37.0 ± 1.44 ‰ and 35.7 ± 1.44 ‰, respectively) ($F_{3,320}$ = 15.5, $p \leq 0.0001$) (Table 5). pH varied significantly across plots; highest pH values were measured in fringe and interior plots (7.00 ± 0.70 and 7.19 ± 0.60, respectively), followed by salt marsh (6.86 ± 0.70), and ecotonal plots (6.78 ± 0.70)

Table 5 Spatial and temporal site characteristics

	Mangroves		Ecotone	Salt Marsh
	Fringe	Interior	Fringe	Interior
Salinity (ppt)	29.4 ± 1.17[a]	25.1 ± 1.44[a]	37.2 ± 1.44[b]	35.7 ± 1.44[b]
Soil pH	7.01 ± 0.06[ab]	7.19 ± 0.06[a]	6.76 ± 0.07[c]	6.86 ± 0.07[bc]
Summer - air temp (°C)	27.8 ± 0.13[a]	27.6 ± 1.99[a]	30.1 ± 0.14[b]	29.9 ± 0.14[b]
Winter - air temp (°C)	21.9 ± 0.19[c]	22.0 ± 0.23[c]	21.7 ± 0.17[c]	22.1 ± 0.22[c]

Different letters denote significance across rows. Values are mean ± SE. Summer air temperature values are the mean of daily high temperatures from June – September. Winter air temperature values are the mean of daily high temperatures from December – March

($F_{3,50}$ = 7.17, p = 0.0004). Seasonality also significantly affected pH ($F_{3,305}$ = 42.1, p ≤ 0.0001) (Table 5). There was a significant interaction between geographical plot location and seasonality on temperature ($F_{7,12,331}$ = 31.2, p ≤ 0.0001). In the summer, salt marsh and ecotone plots were significantly hotter than mangrove plots, while there was no significant difference in the winter months (Table 5).

Discussion

Coastal wetlands along the Atlantic coast of Florida comprise a significant C stock. Mangrove ecosystem C storage (307 Mg C ha^{-1}) was low compared to reports from Mexico (Adame et al. 2013), the Dominican Republic (Kauffman et al. 2014), and the mean presented in a recent synthesis by Alongi (2014). However, it is similar to the Bangladesh Sundarbans (Rahman et al. 2015), Mozambique (Stringer et al. 2015), as well as a smaller scale study done in the Florida salt marsh – mangrove ecotone (Doughty et al. 2016) (Table 6). Total mangrove C stocks along the 342 km latitude studied were lower than in equatorial regions as that mangrove forest C varies greatly among different geographic locations and forest structure (e.g. Donato et al. 2011; Bhomia et al. 2016). Forest structure varies due to plant productivity, which can result

from tree age, species composition, climate, geomorphology, and tidal influences (Bouillon et al. 2008; Lovelock et al. 2010; Alongi 2014). The broad range of total ecosystem C stocks in Florida (122–320 Mg C ha^{-1}) (Fig. 3) reflected the wide array of sites and different geomorphic settings sampled in this study, and suggests an equally broad range of C sequestration potential.

Variability in total C stocks was both a function of aboveground structure and soil C storage. Interior mangrove C stocks were 2.6 times greater than salt marsh C stocks and 1.7 times greater than ecotonal C stocks (Fig. 3), likely driven by the high density of tall trees and large soil C pool in interior mangrove plots. Ecotonal plots had 1.5 times more trees than interior plots, yet the interior trees were 3.7 times taller than those in ecotonal plots. Variability in mangrove tree density and structure represents differences in the characteristics of sampled locations such as geomorphic settings, rainfall, tides, and the availability of fresh water and nutrients (Odum et al. 1982; Krauss et al. 2008). Additionally, interior mangroves are not usually exposed to direct tidal flushing due to their landward location and as a result are sinks for organic matter, nutrients and sediment (Woodroffe 1992). Belowground biomass does not make up a large C component in this study, yet it is significantly greater in mangroves than in ecotonal and salt marsh vegetation (Fig. 3), indicating that mangroves may

Table 6 Comparison of mangrove ecosystem C stocks around the world with present study

Site	Mangrove C stocks (Mg C ha⁻¹)	Source
Florida	307	This study
Florida	53–122	Doughty et al. 2016
Sundarbans	159–360	Rahman et al. 2015
Mozambique	373–360	Stringer et al. 2015
Honduras	570–1222	Bhomia et al. 2015
Yucatan Peninsula	631	Adame et al. 2013
Global Synthesis	700	Alongi 2014
Dominican Republic	706–1131	Kauffman et al. 2014
Indo – Pacific Region	990–1074	Donato et al. 2011

Values shown are means

have higher rooting volumes than salt marsh. This has also been shown in the salt marsh – mangrove ecotone in Texas; mangroves produce greater root volumes over greater depths and have more complex aboveground structures than salt marsh plants (Comeaux et al. 2012; Duarte et al. 2013). Conversely, while the combination of biomass components made up a large part of the total C stock, the majority of C was stored in soils.

Wetland soils were the largest repository of C stocks in this study, as has been documented in other studies (Donato et al. 2011; Kauffman et al. 2011; Alongi 2012; Adame et al. 2013; Kauffman et al. 2014). Soil C stocks made up 51–98% of total C stocks across vegetation types. Interior mangroves contained more soil C than ecotone and salt marsh habitat (58% and 52% more, respectively) (Fig. 3), which may be due to the recent encroachment of mangroves into the study area, as well as the small stature and patchy extent of ecotonal mangroves. Belowground C is likely slow to change with mangrove encroachment (Perry and Mendelssohn 2009; Comeaux et al. 2012; Henry and Twilley 2013) and lag behind aboveground C storage on the expansion front. Henry and Twilley (2013) found that modification from *S. alterniflora* marshes to scrub *A. germinans* stands did not affect soil development or chemistry in a coastal Louisiana wetland over a 50-year period. Perry and Mendelssohn (2009) reported similar findings over a 15-year period. Hence, differences in total C stocks between ecotonal mangroves and salt marsh in this study can be attributed to large differences in aboveground biomass and were not significantly influenced by soil C stocks. Soil C was only 1.5 times greater in ecotonal mangroves than in salt marsh, suggesting that soil C has a lower impact than aboveground biomass to total C stocks in areas undergoing rapid change. A synthesis of shrub encroachment into terrestrial grasslands has shown that while structural change may have mixed effects on ecosystem functional traits, significant increases in aboveground and soil C pools are common (Eldridge et al. 2011). While ecosystem C stocks varied across vegetation types, they also varied across latitudes due to the inherent structural change of dominant species along the Atlantic coast of Florida.

Total C stocks were highest in lower latitudes (26 °N – 27 °N) and decreased with an increase in latitude (28 °N – 29 °N), due to the structural change in species. Mangroves in this study decreased in height and density with increasing latitude, while salt marsh species decreased with a decrease in latitude (Table 1). Mangrove density ranged from 5000 trees ha^{-1} in southern plots, to 29,000 trees ha^{-1} in northern plots, likely indicative of differences in forest composition, climate, hydrology, geomorphology, successional stage, and history of disturbances (Fromard et al. 1998; Cohen et al. 2013). In this study, we observed smaller amounts of biomass and C stocks at higher latitudes compared to lower latitudes (Table 3), which supports the assertion that divergent growth forms have

reduced capacity for C storage (Doughty et al. 2016). Additionally, colder winter temperatures in northern sites likely slows growth of mangroves in comparison to the subtropical mangroves of the southern plots. If regional winter warming continues, we may see an increase in northern mangrove cover, thereby increasing C storage potential of these dynamic ecosystems.

Mangrove and salt marsh species currently cover 38,542 ha of coastal wetland habitat along the 342 km Atlantic coastline documented in this study, which averages 215 Mg C ha^{-1}. There is 32% more C in mangrove aboveground biomass than in salt marsh vegetation which explains why mangroves, which only cover 31% of the land area, store 44% of the total C. If mangroves are able to expand into all current salt marsh habitat, mangrove area would increase by 26,426 ha, and there would be a 26% increase in total C stock of the system. Total C would go from 8,290,005 Mg C to 10,436,113 Mg C and would equate to an average C stock of 271 Mg C ha^{-1}. This expansion would potentially increase previous salt marsh habitat area C stock by 81.2 Mg C ha^{-1}; a 48% increase in C storage. This study suggests that as mangroves progress into areas that were once historically dominated by salt marsh, large differences in biomass will be the main driver behind rapid initial increases to C storage. As coastal wetlands saturate with mangroves, C storage will increase due to structural complexity and productivity. Additionally, these coastal wetlands store 8.29×10^6 Mg C, which is equivalent to 3.04×10^7 Mg of CO_2. A 26% increase in C storage would increase CO_2 sequestration to 3.83×10^6 Mg of CO_2. Hence, while mangroves are declining worldwide (Polidoro et al. 2010) increases in C capture, due to increases in mangrove density and extent, may potentially create a negative feedback to global warming.

Carbon stock estimates provided may be subject to limitations, such as sampling the entire soil profile and scaling up to large areas, and it is possible that soil C storage in this study may have been underestimated due to variations in mangrove organic soil depth (Donato et al. 2011). Belowground biomass estimates may also be underestimated as they are generally analogous to aboveground biomass due to the use of allometric equations. Despite potential underestimations, this study provided us with an excellent opportunity to characterize the extensive Atlantic coastline of Florida. This comprehensive and dynamic coastline is at the forefront of environmental change and our work highlights the sequestration potential of this important ecosystem.

Our results support the conclusion of Donato and others (2011) that the unique environment of mangrove forests, including those measuring less than 1 m in height contain exceptionally high C stocks. Our findings suggest that vegetation expansion can cause dramatic increases in wetland C sequestration due to increases in aboveground biomass, which have implications for the role of blue C and the C sink

capacity of coastal wetlands along Florida's Atlantic coast. We believe this analysis to be the most comprehensive study in Florida to date, and it brings to light patterns and trends in C storage along a latitudinal gradient. This work provides baseline C stock estimates for future studies. As mangrove size and extent increase with continued encroachment in a warming climate, impacts to soil C stocks could intensify (Perry and Mendelssohn 2009; Comeaux et al. 2012; Henry and Twilley 2013) as total C stocks and C concentration are positively correlated with mangrove stand age (Lunstrum and Chen 2014). By strengthening the science supporting the storage potential of coastal ecosystems, C sinks, and our understanding of associated biogeochemical processes, the ability to identify and manage priority areas for conservation and restoration will greatly improve.

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