

Mangrove Range Expansion Rapidly Increases Coastal Wetland Carbon Storage

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Abstract The climate change-induced expansion of mangroves into salt marshes could significantly alter the carbon (C) storage capacity of coastal wetlands, which have the highest average C storage per land area among unmanaged terrestrial ecosystems. Mangrove range expansion is occurring globally, but little is known about how these rapid climate-driven shifts may alter ecosystem C storage. Here, we quantify current C stocks in ecotonal wetlands across gradients of marsh- to mangrove-dominance, and use unique chronological maps of vegetation cover to estimate C stock changes from 2003 to 2010 in a 567-km² wildlife refuge in the mangrove-salt marsh ecotone. We report that over the 7-yr. period, total wetland C stocks increased 22 % due to mangrove encroachment into salt marshes. Newly established mangrove stands stored twice as much C on a per area basis as salt marsh primarily due to differences in aboveground biomass, and mangrove cover increased by 69 % during this short time interval. Wetland C storage within the wildlife

refuge increased at a rate of 2.7 Mg C ha⁻¹ yr⁻¹, more than doubling the naturally high coastal wetland C sequestration rates. Mangrove expansion could account for a globally significant increase of terrestrial C storage, which may exert a considerable negative feedback on warming.

Keywords Climate change · Range expansion · Ecotone · Carbon storage · Mangrove · Salt marsh

Introduction

Coastal wetlands lie at the intersection of land and sea and are highly susceptible to the impacts of climate change. Increasing temperatures, rising seas, and a higher frequency and intensity of storm events have had observable impacts on coastal wetlands and will continue to threaten the status of coastal systems worldwide (Cahoon 2006; Day et al. 2008; Duarte et al. 2013). Salt marshes, mangroves and seagrass beds are estimated to cover as much as 1,152,361 km² of Earth's surface, yet, 2.9–5.9 % of the area covered by these systems is lost annually to natural and anthropogenic forces (McLeod et al. 2011). The continued loss of coastal ecosystems will have far-reaching ecological and economic impacts (Duarte et al. 2008). Vegetated coastal habitats are listed among the most valuable ecosystems in the world (Costanza et al. 1997) because they provide key ecosystem services such as coastal protection, erosion prevention, nutrient cycling, fisheries maintenance and high rates of carbon (C) sequestration (Barbier et al. 2011).

Coastal wetlands are highly efficient C sinks, sequestering photosynthetically derived “green carbon” in living biomass and soils and trapping “blue carbon” from oceanic sources in sediments (McLeod et al. 2011; Nellemann et al. 2009). Global estimates of wetland soils indicate that mangroves

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store substantially more belowground C than salt marshes despite salt marshes having a higher estimated global C burial rate (Duarte et al. 2013). Furthermore, belowground mangrove C stores may remain intact for thousands of years if undisturbed (Nellemann et al. 2009). Mangroves also have a disproportionately large contribution to global wetland C stocks in biomass and soils despite occupying only a small percentage of coastal areas (Alongi 2014; Hutchison et al. 2014), and the potential for aboveground C storage in woody mangrove vegetation is markedly greater than herbaceous salt marsh species (McKee and Rooth 2008). Averages of global C sequestration rates and stocks have been compiled individually for salt marsh and mangrove ecosystems (Alongi 2014), but it is unclear how C storage will change as mangroves encroach into salt marshes, as is occurring in salt marsh-mangrove ecotones worldwide (Saintilan et al. 2014).

Further, assessing C storage in ecotones where mangroves are currently expanding into salt marshes allows for an examination of changing C dynamics at one location. Ecotones are highly sensitive to changes in environmental conditions and are therefore more likely to exhibit extreme responses to climate change (Risser 1995), such as rapid salt marsh to mangrove conversion. The vegetation from these adjacent ecosystems are structurally distinct, with inherently different C storage capacity (Alongi 2014; Duarte et al. 2013) and C sequestration rates (Lovelock et al. 2014), indicating that dominant vegetation cover conversion in a given area will alter the total C storage of that area. Furthermore, the C storage capacity of temperate ecotonal mangroves may be substantially lower than tropical mangroves due to a reduction in mangrove height with latitude (Morrissey et al. 2010). The total C storage per area of an ecotonal coastal wetland may depend on the structural characteristics within and among vegetation types, as well as the fluctuations in extent of each vegetation type.

The effects of plant range shifts on ecosystem C storage have been extensively studied in similar herbaceous-to-woody plant conversions. For the majority of species and ecoregions of the North American grasslands, woody encroachment results in the net gain of ecosystem C storage (reviewed by Barger et al. 2011) and is often extensive and rapid (e.g., Asner et al. 2003; Neff et al. 2009). Woody encroachment in grasslands throughout the U.S. reveal sequestration rate estimates of 0.10–0.13 Pg C yr⁻¹ which lead to increases in overall C stocks (Houghton et al. 1999; Pacala et al. 2001; Tilman et al. 2000). Increases to ecosystem C storage in woody plant-invaded grasslands can be partly attributed to higher aboveground biomass of woody vegetation as compared to herbaceous grasses (Asner et al. 2003; Scharenbroch et al. 2010). The relationship between woody invasions and aboveground biomass carbon is positively correlated, but the impacts to belowground carbon storage are mixed (Gill and Burke 1999; Jackson et al. 2002) and depend on many environmental (e.g., temperature, precipitation) and

species-specific (e.g., productivity, litterfall chemistry, decomposition rates) factors (Gill and Burke 1999; Neff et al. 2009). Coastal wetlands and grasslands are experiencing similar woody encroachment, but under very different environmental circumstances; coastal wetlands are impacted by flooding, anoxic soils, and salinity. Ecosystem C storage dynamics in coastal wetlands undergoing woody encroachment within these distinct ecotonal communities could differ substantially from upland sites where trees and shrubs are also encroaching.

The expansion and contraction of species geographic ranges due to climate change (Parmesan and Yohe 2003; Walther et al. 2002) are exemplified by the poleward expansion of mangrove range limits on a global scale (Saintilan et al. 2014). In the Southeastern United States, the expansion of mangroves into higher latitudes is driven predominantly by the declining frequency of severe freeze events (Osland et al. 2013). Recent findings suggest that -4 °C constitutes the threshold of mangrove freeze tolerance and is closely linked to mangrove extent in Florida (Cavanaugh et al. 2014a). In the absence of temperature constraints and geographic barriers on the Atlantic coast of Florida, mangroves have surpassed historical limits at Port Orange (29.13843° N) (Hawks 1887), and the pioneer black mangrove *Avicennia germinans* has been reported as far north as the Guana Tolomato Matanzas estuary (30.1103° N), followed by the red mangrove, *Rhizophora mangle* (29.9393° N), and the white mangrove, *Laguncularia racemosa* (29.7251° N) (Williams et al. 2014).

Fewer freeze-related disturbances in Florida have resulted in increased mangrove extent over the past several decades, which coincides with the overall trend of poleward mangrove range expansion (Saintilan et al. 2014). However, recent mangrove expansion in this region may be due to re-emergence from previous populations (Cavanaugh et al. 2014b; Giri and Long 2014), as evidenced by freeze-induced die-backs of mangroves in the 1980's (Giri et al. 2011a; Provanca et al. 1986). In addition to air temperatures, mangrove extent responds to environmental factors such as erosion, land subsidence and aggradation causing additional fluctuations in mangrove extent over shorter temporal scales (Giri and Long 2014). Regardless, long-term, continual mangrove expansion in Florida is supported by the salt marsh-to-mangrove conversion of Tampa Bay wetlands at a rate of 72 % over 125 years (Raabe et al. 2012). At the northernmost mangrove limit in Florida, mangrove-dominated land area has doubled since 1986 (Cavanaugh et al. 2014a), and dominant plant cover changes of this magnitude have the potential to significantly alter landscape C storage (Comeaux et al. 2012; McKee and Rooth 2008).

We coupled field-based assessments of ecosystem C stocks with a unique chronology of remote sensing-derived land cover maps to (1) measure C stocks in a representative ecotonal wetland, (2) quantify mangrove encroachment on a fine spatial scale, and (3) assess how wetland C stocks could change

due to mangrove range expansion from 2003 to 2010. We quantified several C stocks, including aboveground biomass, belowground biomass and soil, for a representative ecotonal plant community within the Merritt Island National Wildlife Refuge of Florida, where mangrove encroachment has been ongoing (Taylor, pers. comm.). In this study, for the first time, we integrated field and geospatial approaches to produce landscape level estimates of C stocks among salt marsh and mangrove vegetation spanning both time and space that will provide insights into the C storage dynamics of coastal wetlands undergoing mangrove range expansion across the globe.

Methods

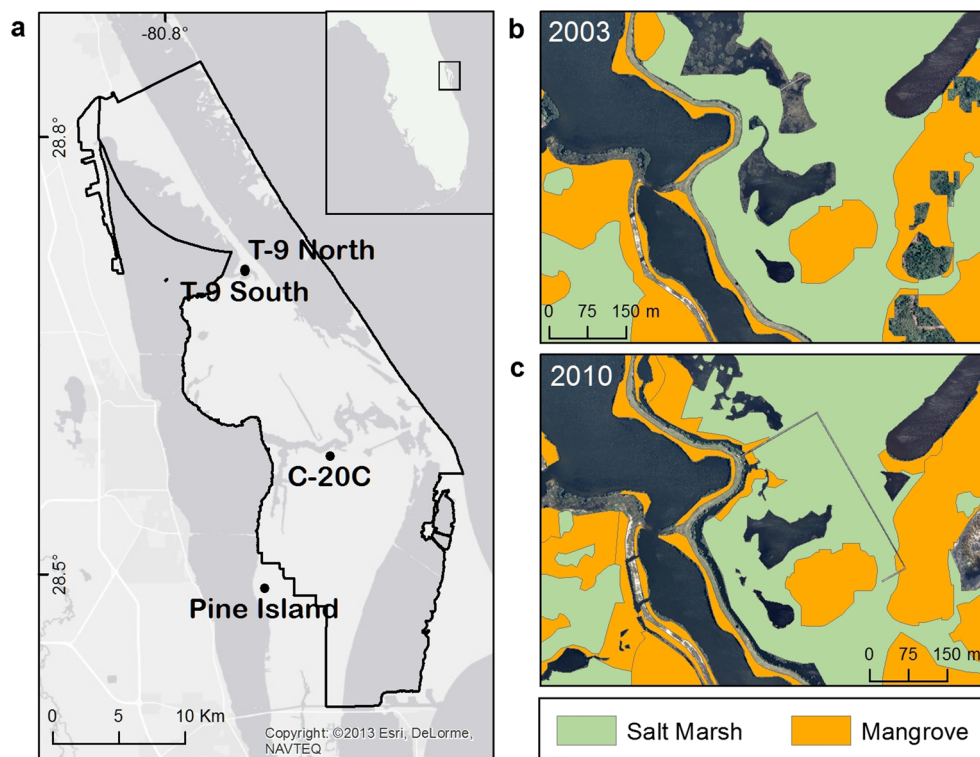
Site Description

We explored changes in carbon stocks over a 7-year period at the salt marsh-mangrove ecotone (28.3311° N - 30.2333° N) along the eastern coast of Florida. Field sampling was conducted at three sites (C-20C, T-9 North and T-9 South; named by Brevard County Mosquito Control) within the Kennedy Space Center (KSC) and the overlying Merritt Island National Wildlife Refuge (MINWR) (Fig. 1a, Online Resource 1). A fourth site was chosen to the south in the Pine Island Conservation Area (28.4917° N, 81.7274° W) to account for further latitudinal variation among wetland communities. Site selection was influenced by accessibility via

KSC infrastructure, boat or traversing wetlands. This area represents an ecotonal community undergoing rapid climate-driven vegetation changes following severe freeze events in the early 1980's (Provancha et al. 1986). Mean monthly air temperatures range from 10 °C in winter to 33.3 °C in summer; minimum monthly air temperatures from 1973 to 2010 ranged from -23.9 °C to 17.8 °C with an average of 0.4 °C. Mean annual precipitation is ~137 cm with the heaviest rainfall occurring from June to September. Soils within MINWR consist of organic debris, and/or silty clays over sand and irregularly stratified mixed sand and shell. Soil salinity ranged from 30.0–50.8 ppt. MINWR is separated from the mainland by the Indian River Lagoon (IRL), a 260 km long estuary of depths ranging from 0.5 to 3.0 m over muddy and sandy substrates (Vaslet et al. 2012). The tides within the IRL are microtidal, which vary between 0.1 m and 0.7 m (Smith 1987).

In May 2013, field sites were chosen to encompass three classes of coastal wetland vegetation: mangrove, salt marsh and transitional (i.e., areas of salt marsh with encroaching mangroves). Salt marsh and mangrove species exist largely in monospecific patches, creating a mosaic landscape of vegetation classes across the four sites. Focal species within each vegetation class reflect the dominant species at each site including three mangrove species (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*) and four salt marsh species (*Spartina alterniflora*, *Distichlis spicata*, *Batis maritima* and *Salicornia bigelovii*). Transitional plots

Fig. 1 Representative ecotonal wetland at MINWR undergoing climate-induced land cover shifts. **a** Sampling sites within the Merritt Island National Wildlife Refuge, FL. Mangrove and salt marsh vegetation cover for **b** 2003 and **c** 2010 extracted from land cover maps and overlaid on multispectral digital orthophotography



consisted of *D. spicata* salt marsh and mangrove seedlings/juveniles, indicating that mangrove establishment among other salt marsh species was not common at our sites. Sampling at each site was influenced by the availability and accessibility of each vegetation class.

The mangrove vegetation in this area varied in growth form (height and architecture), which may differ due to location, nutrient availability, soil characteristics, age and freeze tolerance (Castañeda-Moya et al. 2013; Osland et al. 2014; Turner et al. 1995). Mangroves under 2 m in height existed in two architecture types, sapling and scrub, which exhibit different growth characteristics (Feller and Mathis 1997). Scrub mangroves were characterized by short, stunted stature, small internodal lengths, and appeared to be relatively old trees (Feller 1995); these mangroves were commonly referred to as “dwarf” mangroves in previous literature (Feller et al. 2007). Sapling mangroves were relatively young plants which exhibited vigorous growth as indicated by long internodes and minimal axial branching (Feller and Mathis 1997).

Field Assessment of Carbon Stocks in a Representative Ecotonal Community

In order to assess C stocks in herbaceous plant species, we established a set of three 1-m² plots within stands of salt marsh focal species ($n_{\text{set}} = 10$, $n_{\text{plots}} = 30$) and within transitional areas ($n_{\text{set}} = 3$, $n_{\text{plots}} = 9$). In dominant stands of each mangrove species, we established a set of three 9-m² plots ($n_{\text{set}} = 9$, $n_{\text{plots}} = 27$). In total, we sampled 66 plots of ecotonal vegetation. Sample plots were sized to quantify biomass and C at an appropriate scale for each vegetation class.

We collected and subsampled a soil core (5 cm diameter × 30 cm depth) using a custom-made beveled peat corer for belowground biomass and soil C analysis in each plot. The assessment of belowground C stocks was limited to a depth of 30 cm for all vegetation classes due to the shallow organic soil horizons at all sites, which ensured conservative belowground biomass estimates and standardized the comparison between vegetation types that may have substantially different rooting depths. Soil cores were subsampled for belowground biomass analysis and percent C analysis (described below).

Belowground biomass, or roots, was separated from soil by washing a core subsample in a 2-mm sieve. Flow-through matter was collected by a 0.5-mm sieve and placed in water to separate sediment and live fine roots. Roots were dried at 60 °C for 72 h and weighed to determine belowground biomass to a depth of 30 cm. Roots were ground in a Wiley Mill (Thomas Scientific, Swedesboro, NJ) equipped with 4.25 mm mesh filter in preparation for C:N analysis. All percent C analyses were conducted on a TruSpec C:N analyzer

(LECO, St. Joseph, MI). Percent C was multiplied by biomass to obtain C stored in belowground biomass.

The remaining soil core was further divided into organic and mineral layers, and a section of the intact total core was also preserved. All soil samples were dried at 105 °C for 14 days and massed. We calculated soil bulk density (g cm^{-3}) by dividing the oven dried sample mass by the sample volume. Dried samples were ground using a mortar and pestle to ensure homogenization. Percent C was determined using C:N analysis and was multiplied by soil bulk density to determine total soil C in the top 30 cm of soil.

Aboveground biomass estimates for salt marsh plant species were determined via destructive harvesting from one 0.1 m² subplot chosen at random within the 1 m² sampling plots. We found that 0.1 m² was an adequate sampling size to represent the density of salt marsh species based on observations of homogeneity at the sites. Aboveground shoots were dried at 60 °C for 72 h, massed, and ground in preparation for C:N analysis. Percent C was multiplied by biomass to estimate total aboveground C in salt marsh vegetation.

Aboveground biomass in mangroves was determined using allometric equations obtained from previous research on temperate mangroves in South Florida (Ross et al. 2001; Smith III and Whelan 2006) (Online Resource 2). Allometric equations were carefully selected to reflect the range of heights and architectures of the ecotonal mangroves at our field sites. Mangrove vegetation was sub-categorized by species into multiple classes based on maximum height (short: < 2 m vs. tall: 2–7 m) with the short height class being further differentiated based on architecture (sapling vs. scrub). We used the allometric equations developed by Smith & Whelan (2006) to calculate biomass for mangroves in both the sapling and tall class, because these classes represent a similar architecture type independent of height. The majority of mangroves within the tall class were single stemmed, but trees with multiple stems were treated as individual trees. The allometric equations in Ross et al. (2001) were applied to scrub mangroves. A C concentration factor of 0.48 (Kauffman and Donato 2012) was then multiplied by biomass estimates to determine total aboveground C stocks.

Total aboveground C for transitional sampling plots was obtained by combining aboveground C estimates for salt marsh (described above) and mangrove seedlings. To determine aboveground biomass in mangrove seedlings, we developed allometric equations for 24 seedlings ranging in height from 5 cm to 107 cm. Seedlings were collected in transitional areas surrounding the sampling plots. Seedlings were measured for height and basal diameter, and were dried at 60 °C for 7 d and massed. A multiple linear regression analysis yielded the following allometric equation to best predict aboveground biomass ($R^2 = 0.93$):

$$\ln(\text{AB}) = 1.6367 \cdot \ln(\text{D}_b) + 1.3045 \cdot \ln(\text{H}) - 2.8853;$$

where AB is aboveground biomass, D_b is basal diameter and H is height. Aboveground biomass in seedlings was multiplied by a C concentration factor of 0.48 to determine C in young mangroves.

Average C estimates (Mg ha^{-1}) were determined for the vegetation classes and mangrove architectures to aid in the land cover analysis (described below). Comparisons of C and biomass assessments between vegetation classes and among mangrove architectures were tested using two-way ANOVAs; across-site comparisons of belowground C were tested using two-way paired t-tests. Data were log-transformed to meet assumptions of homogeneity of variances as needed.

Estimating Land Cover Change and the Relationship to Carbon Stocks

Land cover maps of MINWR for 2003 and 2010 were provided by NASA's Earth Systems Modeling Department at the Kennedy Space Center, FL in the form of geodatabase feature dataset compatible with ArcMap © 10.1 (ESRI, Redlands, CA). Mapping was conducted using multispectral digital orthophotography and airborne Light Detection and Ranging (LiDAR) data together with expert knowledge on life-form signatures based on vegetation structure and height, as well as information on water level and salinity. Land cover classes were delineated manually on-screen to create highly accurate geodatabase feature classes (e.g., a layer of polygons) of regions that correspond to each land cover class (Fig. 1b, c). Airborne LiDAR-derived Digital Terrain Model (DTM) and Digital Surface Model (DSM) data from 2007 were also provided in support of the analysis. All processing and analysis of land cover and ancillary remote sensing data sets were performed using ArcMap© 10.1 (ESRI, Redlands, CA).

We extracted the land cover classes of relevance to our analysis, which included the “mangrove”, “salt marsh”, and “wetland scrub-shrub” classes. Field observations of sapling and scrub mangroves within areas mapped as wetland scrub-shrub prompted us to reclass the wetland scrub-shrub areas as mangrove and append them to the existing mangrove class in order to account for mangroves of short stature (i.e., less than 2 m tall).

We also developed a correction factor to address the observation of unlikely change trajectories from 2003 to 2010 (e.g., salt marsh to mangrove is possible while cabbage palm to mangrove is not). This analysis accounts for possible errors in mapping from 2003 to 2010 that may have arisen from the use of alternative data sources (e.g., airborne LiDAR) between the two periods leading to the increased detectability of mangroves. Classification errors associated with the land cover maps were manually assessed using a set of 1000 points randomly distributed within the extent of the area classified as

mangrove in 2010. The same set of points was overlaid onto the 2003 land cover map to determine how these areas were previously classified.

We found that 7.9 % of the change trajectories were unlikely, indicating that the mangrove class in 2003 was misclassified as other woody vegetation and, hence, underestimated in terms of coverage. Based on these findings, we increased the areal estimate of mangrove cover in 2003 by 7.9 % prior to joining this class with the scrub-shrub class in order to prevent overestimating the increase in mangrove extent from 2003 to 2010. As part of this analysis, we also noted that 11.1 % of the points were classified as wetland scrub-shrub in 2003, but were later classified as mangrove in 2010, further supporting the combination of these classes.

Within the mangrove class, we classified individual polygons based on our allometrically-defined height classes to reflect short (i.e., saplings and scrubs <2 m) and tall (>2 m) mangroves in both the 2003 and 2010 land cover maps. First, we generated a vegetation height raster by subtracting the 2007 airborne LiDAR-derived Digital Terrain Model (DTM) from the Digital Surface Model in ArcMap© 10.1. The maximum height value within each polygon was then determined, which allowed for the subdivision of the mangrove land cover class into height classes. Maximum height was used to account for the tallest mangroves within a polygon to be consistent with our classification of sampling plots from field observations. The resulting mangrove height classes derived from the vegetation height model would underestimate mangrove biomass for 2010 land cover (i.e., mangrove stands would only increase in height from 2007 to 2010) and would overestimate mangrove biomass for 2003 land cover (i.e., mangrove stands would increase in height from 2003 to 2007). Ultimately, this ensures a conservative estimate of biomass change from 2003 to 2010. The data layer resulting from this process enabled us to more accurately and conservatively extrapolate our height-based C stocks estimates to the landscape level.

We calculated the areal extent for salt marsh and two mangrove classes (sapling/scrub and tall) in MINWR for 2003 and 2010. To estimate total wetland C stocks, we multiplied our field-based estimates of C stocks by the extent of salt marsh and mangrove classes (sapling/scrub and tall). Then, we calculated total land cover conversion from salt marsh to mangrove within MINWR and the associated changes in C stocks.

Results

Mangroves consistently stored more total C and accounted for more biomass than salt marsh and transitional vegetation classes (Table 1, Fig. 2). Total C stocks, i.e., combined biomass (above- and belowground) and soil C, per area in mangrove

Table 1 Biomass and Carbon Storage in an Ecotonal Wetland

	Vegetation Class				Mangrove Architecture Class			
	Mangrove	Transitional	Salt Marsh	<i>p</i> -value	Sapling	Scrub	Tall	<i>p</i> -value
Total Biomass (Mg ha ⁻¹)	139 ± 25	28 ± 2	33 ± 4	***0.0001	80 ± 20	89 ± 20	208 ± 20	*** < 0.0001
Aboveground Biomass	114 ± 23	23 ± 2	26 ± 4	***0.0004	62 ± 27	61 ± 4	179 ± 16	*** < 0.0001
Belowground Biomass	25 ± 8	5 ± 0	7 ± 1	*0.036	18 ± 5	28 ± 16	29 ± 16	0.175
Total Carbon (Mg C ha ⁻¹)	122 ± 16	53 ± 5	61 ± 4	**0.001	89 ± 16	87 ± 4	163 ± 19	*** < 0.0001
Aboveground Biomass Carbon	55 ± 11	10 ± 1	8 ± 1	*** < 0.0001	30 ± 13	29 ± 2	86 ± 8	*** < 0.0001
Belowground Biomass Carbon	10 ± 3	2 ± 0	3 ± 1	0.0539	7 ± 2	10 ± 6	12 ± 7	0.232
Soil Carbon	57 ± 6	41 ± 5	49 ± 5	0.597	53 ± 7	47 ± 3	66 ± 11	0.395

Biomass and carbon storage (\pm s.e.m.) for the wetland vegetation classes and mangrove architecture classes. Note that *p*-values are reported for two-way ANOVAs of biomass or carbon component for both Vegetation and Mangrove Architecture classification schemes. Asterisks indicate varying significance: * = 0.05, ** = 0.001, *** = 0.0001

vegetation (122 ± 16 Mg C ha⁻¹) was roughly twice that of either salt marsh (61 ± 4 Mg C ha⁻¹) or transitional (53 ± 5 Mg C ha⁻¹) ($p < 0.001$).

Aboveground biomass in mangroves was 114 ± 23 Mg ha⁻¹, which was significantly higher than the 26 ± 4 Mg ha⁻¹ observed in salt marsh and 23 ± 2 Mg ha⁻¹ in transitional

vegetation classes ($p = 0.0004$). Similarly, belowground biomass was more than three times higher in mangroves ($p < 0.05$); mangroves contained 25 ± 8 Mg biomass ha⁻¹, while salt marsh and transitional contained 7 ± 1 Mg ha⁻¹ and 5 ± 0 Mg ha⁻¹, respectively.

Total belowground C, which included both belowground biomass and soil C, was 57 ± 6 Mg C ha⁻¹ in mangroves, 49 ± 5 Mg C ha⁻¹ in salt marsh and 41 ± 5 Mg C ha⁻¹ in transitional and did not differ significantly between vegetation classes. Within a given site, mangroves contained significantly higher belowground C than salt marshes ($p < 0.05$) attributed to greater belowground biomass. Across sites, belowground biomass C was three times higher in mangroves but was not found to differ significantly from neighboring salt marsh ($p = 0.054$). Soil organic layer depth and organic layer C stocks varied across sites and showed no significant differences between mangroves and salt marshes (Table 2), suggesting that local wetland conditions, such as hydrology, may be a more important driver of soil organic C dynamics.

For the purpose of scaling to the landscape level, we quantified total C stocks and biomass according to mangrove architecture (Table 1). Tall mangroves (> 2 m) stored a total of 163 ± 19 Mg C ha⁻¹, whereas scrub mangroves stored 87 ± 4 Mg C ha⁻¹ and sapling mangroves store 89 ± 16 Mg C ha⁻¹. For both total biomass and total C stocks, tall mangroves were found to be significantly greater than sapling and scrub mangroves ($p < 0.0001$), while there was no statistical difference between sapling and scrub mangroves. All mangrove architecture classes stored higher amounts of total C than saltmarsh (61 ± 4 Mg C ha⁻¹) and transitional (53 ± 5 Mg C ha⁻¹) classes. Mangrove species did not have a significant effect on total C stocks, biomass, or soil C stocks, which may be due to the uneven distribution of mangrove architectures within each species at our field sites.

We used chronological land cover maps of MINWR to quantify the extent of salt marsh and mangroves in 2003 and in 2010 (Fig. 3). In 2003, mangroves occupied only 1516 ha,

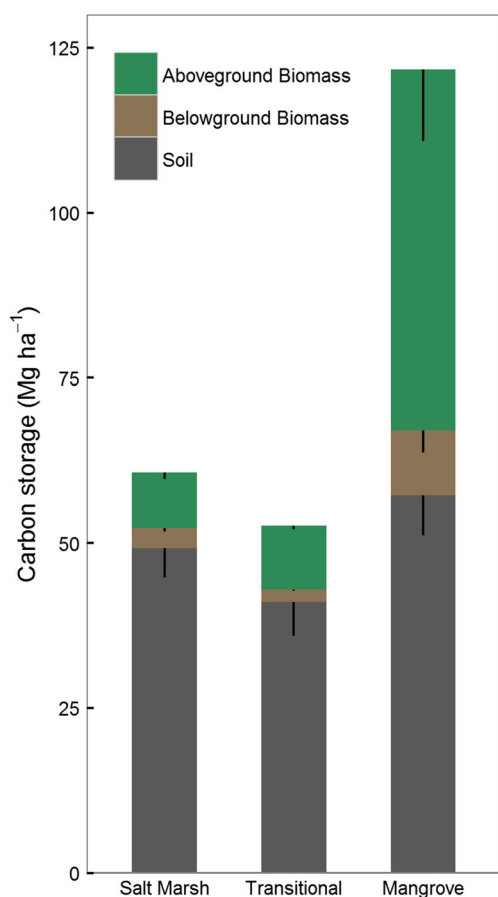


Fig. 2 Carbon stocks in mangroves, salt marsh and transitional vegetation. Carbon stock values reflect averages across sites and error bars signify standard error from the mean. Positive error bars are not shown for clarity

Table 2 Belowground Carbon Attributes between Mangroves and Salt Marshes across Sites

	C-20C		T-9 North		T-9 South		Pine Island		<i>p</i> -value
	Mangrove	Salt Marsh	Mangrove	Salt Marsh	Mangrove	Salt Marsh	Mangrove	Salt Marsh	
Belowground Carbon (Mg/ha)	66 ± 11	51 ± 8	65 ± 11	58 ± 5	43 ± 1	41 ± 10	54 ± 11	45 ± 4	0.080
Organic Layer Depth (cm)	3 ± 2	7 ± 1	6 ± 2	7 ± 1	1 ± 1	1 ± 1	2 ± 1	3 ± 0	0.139
Organic Layer Carbon (Mg/ha)	0 ± 0	104 ± 37	57 ± 30	25 ± 18	56 ± 40	32 ± 23	170 ± 32	422 ± 61	0.342
% Carbon in Organic Layer	0 ± 0	16 ± 6	10 ± 4	6 ± 4	9 ± 6	7 ± 5	8 ± 1	26 ± 2	0.333

Belowground carbon storage (\pm s.e.m.) for mangroves and salt marshes at study sites. Note that *p*-values are reported for two-way paired *t*-test of soil components across the sites. No statistically significant differences were detected for the soil components

while salt marsh extent was three times greater, comprising 5182 ha of MINWR wetlands. By 2010, mangrove extent had increased to 2555 ha, while salt marsh extent had declined to 4531 ha.

In 2003, mangroves contained C stocks of 247 Gg while salt marsh accounted for stocks of 314 Gg based on the extrapolation of our field C stock estimates. With a 69 % (1039 ha) increase in mangrove extent by 2010, mangrove C stocks across MINWR increased by 164 Gg for a total of 411 Gg of C stored. Salt marsh extent declined by 13 % (651 ha) from 2003 to 2010, reducing total salt marsh C stocks in MINWR to 275 Gg. Total wetland C stocks in MINWR increased from 561 Gg in 2003 to 686 Gg of C by 2010, a 22 % increase occurring at a rate of 2.7 Mg C ha⁻¹ yr.⁻¹ due to an increase in mangrove extent in this ecotonal wetland.

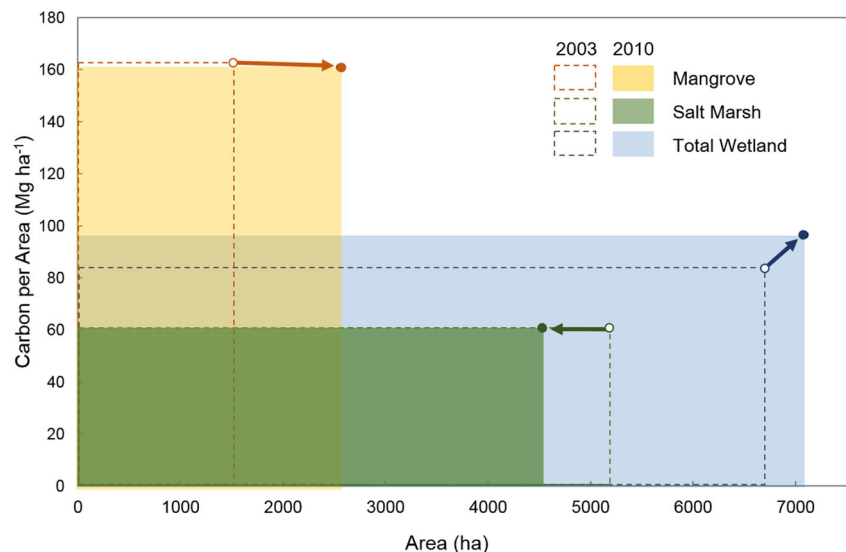
Discussion

We used a field-based approach to assess C stocks within a representative ecotonal wetland community and paired our C stock estimates with a chronology of detailed land cover maps in order to quantify the C storage dynamics associated with

climate-induced land cover changes. Our assessment of land cover change within MINWR was made possible by land cover maps of high spatial resolution (< 1 m), which allowed for the detection of small-scale increases in mangrove extent. The use of a LiDAR-derived vegetation height model enabled us to differentiate between two mangrove height classes at the landscape-level, which increases the accuracy of our extrapolated estimates of landscape C stocks given their clear difference in C storage capacity. We integrated our field-based C estimates with the land cover change analysis to produce conservatively robust estimates of C storage dynamics accompanying mangrove range expansion for a particular region.

In the salt marsh-mangrove ecotone of Florida, we found that mangroves have roughly twice as much total C stocks (Mg ha⁻¹) and biomass (Mg ha⁻¹) as salt marsh and transitional vegetation classes. Global trends of wetland C stocks indicate that mangroves contain higher total ecosystem C stocks than salt marshes, which is primarily driven by soil C stocks (Alongi 2014). Conversely, our findings suggest that the differences in total C stocks between ecotonal mangroves and salt marsh can be attributed to large differences in aboveground biomass and were not significantly influenced by soil C stocks. Belowground biomass C was three times higher in

Fig. 3 Carbon stocks per area changes over 7 years in Merritt Island National Wildlife Refuge. C stocks represented on a per area basis (Mg ha⁻¹) for 2003 (*open circles*) and 2010 (*closed circles*) according to vegetation class. Outlined (2003) and colored (2010) areas reflect total C stocks per vegetation class; directional changes in C stocks from 2003 to 2010 are indicated by arrows



mangroves ($p = 0.054$) and represents about 1/5 of aboveground biomass C. Thus, belowground biomass C likely contributes to our observed ecosystem-level differences in C stocks. However, ecotonal wetlands undergoing rapid range shifts initially display a unique trend where soil C has a lower impact than aboveground biomass to total C stocks.

Aboveground biomass in ecotonal vegetation was influenced by vegetation morphology, especially for temperate mangroves that exist in a spectrum of growth forms and are structurally divergent from tropical mangroves. Mangroves decrease in height with increasing latitude (Morrisey et al. 2010), a pattern that should yield smaller amounts of biomass and C stocks in high-latitude ecotonal wetlands than in lower latitudes. Belowground biomass was slightly higher in mangroves than salt marsh and transitional, indicating that mangroves may have higher rooting volumes than salt marsh, which corroborates reports from the salt marsh-mangrove ecotone of Texas where mangroves can contain up to twice the rooting volume of neighboring salt marsh (Comeaux et al. 2012).

Carbon stocks did not differ significantly between salt marsh and transitional vegetation classes. These findings disagree with estimates of C storage in an arid grasslands undergoing similar woody encroachment where C stocks were highest in forests, followed by transitional areas, and lastly, grasslands (Scharenbroch et al. 2010). However, this result can be attributed to relatively low biomass in mangrove seedlings and the fact that seedlings were only found in sites dominated by *D. spicata*, the salt marsh species with the lowest C stocks of our focal marsh species. Increased sampling of transitional areas may yield higher C stock estimates if mangrove seedlings can be found in association with other salt marsh species with higher C stocks. However, the presence of young mangroves is not evenly distributed for all salt marsh species, which may be influenced by altered hydrology due to mosquito control impoundments (Vogt et al. 2012). Transitional areas are caused by propagule retention in salt marsh, which varies greatly by species due to structural complexity and stem density (Peterson and Bell 2012). Regardless, transitional areas containing newly colonized mangroves are not reliably detected via airborne or satellite remote sensing, and were excluded from our scaling exercise. Differences in C stocks in transitional areas where mangroves are newly encroaching are not yet applicable in scaling C stocks to the landscape-level.

Soil C stocks were not significantly different between the ecotonal wetland vegetation classes, likely due to the recency of mangrove encroachment in the study area, as well as the small stature and patchy extent of ecotonal mangroves. Total belowground C is likely slow to change with mangrove encroachment (Comeaux et al. 2012; Perry and Mendelsohn 2009) and slow initial changes to soil C with woody encroachment has also been observed in other upland ecosystems

(Barger et al. 2011). Throughout the Gulf of Mexico region, mangrove range expansion into salt marsh wetlands has had variable impacts to soil C stocks, C sequestration and other soil properties (Bianchi et al. 2013; Comeaux et al. 2012; Henry and Twilley 2013; Lewis et al. 2014; Osland et al. 2012; Perry and Mendelsohn 2009). In some instances, mangroves have been found to have higher soil organic matter, C, nitrogen (N), and C sequestration rates than *S. alterniflora* (Bianchi et al. 2013; Osland et al. 2012) and *Juncus roemerianus* (Lewis et al. 2014) salt marshes over relatively short periods of encroachment. Other studies indicate that a species shift from *S. alterniflora* to *A. germinans* has not had a significant impact to soil properties, such as organic matter production, decomposition, and C sequestration, even over multi-decadal encroachment periods (Henry and Twilley 2013; Perry and Mendelsohn 2009). Soil C accumulation in young mangrove stands is initially low, and may not establish soil C signatures that are significantly different from salt marsh for decades (Lunstrum and Chen 2014). As mangrove size and extent increases with continued encroachment in a warming climate, the impacts to soil C stocks could intensify (Comeaux et al. 2012; Henry and Twilley 2013; Perry and Mendelsohn 2009), because total C stocks and C concentration are positively correlated with mangrove stand age (Lunstrum and Chen 2014). Higher lignin concentrations in mangrove litter may also improve the stability and residence time of belowground C stocks (Bianchi et al. 2013).

An increase in mangrove extent over a 7-yr. period had a significant impact on large-scale wetland C stocks. Our findings revealed that a 69 % increase in mangrove extent led to a 22 % increase in wetland C stocks. In MINWR, mangrove encroachment into salt marshes yielded a C storage increase at a rate of 2.7 Mg C ha⁻¹ yr.⁻¹, which is among the highest rates associated with woody invasions for terrestrial ecotones in the United States (Barger et al. 2011). Given these C stock increases and projections of future mangrove extent under a warming climate and rising seas (Record et al. 2013), mangrove range expansion into 2169 km² of coastal wetlands along the southeastern U.S. (U.S. Fish and Wildlife Service 2014) could result in the uptake of 26 Tg of C by 2080. The potential increase to wetland C storage resulting from mangrove range expansion in this region is equivalent to half of Florida's annual anthropogenic C emissions (U.S. Environmental Protection Agency 2014).

Global mangrove range expansion will likely continue if climatic warming continues to diminish the frequency of freeze events. In the dispersal stage, mangroves have superior diaspore adaptations, such as increased buoyancy and size compared to salt marsh species, which allow them to disperse farther and remain viable for longer periods (Alleman and Hester 2011; Friess et al. 2012). Additionally, high survival and continued development following exposure to various degrees and durations of low temperatures reveal high cold

tolerance in early mangrove life forms (Pickens and Hester 2011). Facilitation by salt marsh (Friess et al. 2012; Peterson and Bell 2012) and mangroves (Huxham 2010) plays a crucial role in mangrove propagule entrapment, and once established, mangroves exhibit high levels of plasticity in growth and nutrient partitioning to outcompete neighboring salt marsh (Proffitt and Travis 2010; Simpson et al. 2013). When released from temperature constraints, these drivers accelerate mangrove encroachment into new areas, increasing extent and consequently increasing wetland C storage. However, the full range of ecological consequences of climate-induced salt marsh to mangrove conversion has yet to be explored (Osland et al. 2013).

The most important contribution of mangroves may not be their high rates of C sequestration while encroaching into salt marshes, but that conversion from salt marsh to mangroves could render coastal wetlands more resilient to the effects of future global climate change. Coastal wetlands can tolerate sea level rise through landward migration and sediment accretion (Friess et al. 2012); however, the degree to which vegetation can attenuate tidal flow and trap suspended sediment varies with vegetation structure, complexity, and density (Duarte et al. 2013; Friess et al. 2012). Mangroves produce greater root volumes over greater depths than salt marsh plants and have more complex aboveground structures (Comeaux et al. 2012; Duarte et al. 2013). Thus, mangroves may be more likely to sustain intensifying coastal weather events and sea level rise expected with future climatic change through greater trapping and accumulation of soil (Barbier et al. 2011; Bianchi et al. 2013; Comeaux et al. 2012; Gedan et al. 2011). As our work has illustrated, the structural characteristics of wetland vegetation influence biomass and C storage capacity, which may also provide insights into the tolerance of each vegetation type to the effects of climate change.

Because climatic warming is predicted to increase, continued mangrove range expansion along the southeastern U.S. coast is highly likely, suggesting that wetland C storage will continue to increase as the salt marsh-mangrove ecotone extends farther northward and encroaching mangroves mature to generate greater mangrove-dominated areas. While this work is specific to our focal species and region, it may also be representative of similar salt marsh to mangrove conversions occurring worldwide, indicating the need for improved estimates of C storage in local vegetation and fine-scale regional estimates of land cover and C storage dynamics in place of global extrapolations. Our work exemplifies the need to produce regional assessments of land cover change and accompanying changes to C storage.

At regional scales, wetland managers may be able to leverage mangrove restoration projects to both enhance coastal buffering and increase wetland C storage. However, implementing an ecosystems-based approach to management would require that a broad range of ecosystem services are

conserved and that cumulative impacts to the ecosystem are considered (Rosenberg and McLeod 2005). Salt marsh to mangrove conversion would result in the loss of salt marsh ecosystem services (e.g., specialized habitat for fauna), and therefore, whether the overall impacts to wetland ecosystems will be positive or negative remains uncertain (Osland et al. 2013). Regardless, restoration efforts in areas where mangrove and salt marsh habitats have been lost or degraded would improve global C storage (Irving et al. 2011) and recover ecosystem services (Zedler and Kercher 2005) in vegetated coastal wetlands.

At the global scale, our research suggests that wetlands subject to mangrove encroachment (or mangrove rebound from previous freeze-induced die-back) will have the capacity to sequester C at accelerated rates, which will have consequences – as yet largely unknown – for the C cycle. Due to the high variability in current estimates of global extent, C stocks and C sequestration rates in vegetated coastal habitats, it is difficult to calculate the potential uptake of atmospheric CO₂ caused by future mangrove expansion. The estimated global extent of mangroves ranges from 137,760–152,361 km², and that of salt marshes ranges from 22,000–400,000 km² (McLeod et al. 2011; Duarte et al. 2013), and therefore, global estimates of soil C stocks range from 0.4–6.5 Pg in mangroves and 9.4–10.4 Pg in marshes (Duarte et al. 2013). To our knowledge, global estimates of biomass for salt marsh and mangrove ecosystems do not exist. Our study indicates that as mangroves progress into areas that were predominantly salt marsh, large differences in biomass will be the main driver behind rapid initial increases to C storage. As coastal wetland systems saturate with mangroves, we predict that C sequestration rates due to encroachment will decrease, while C sequestration rates due to productivity and sediment accumulation will increase. Global C burial rates also pose uncertainty due to the high variability in estimates for mangroves (31–34 Tg C yr⁻¹) and salt marsh (5–87 Tg C yr⁻¹) (McLeod et al. 2011). Regardless, coastal wetlands have the capacity to store large amounts of C over the short term (decennial) in biomass and long term (millennial) time scales in sediments (Duarte et al. 2005; McLeod et al. 2011).

The fate of future coastal wetlands is subject not only to mangrove range expansion but to many other biotic and abiotic factors, which may also have an effect on the sustainability of wetland C storage. Increases to atmospheric [CO₂] could have effects on photosynthetic rates and water use efficiency, which ultimately affects plant growth (McKee et al. 2012). Sea level rise poses a potential threat to wetland C stores unless mangroves and salt marshes are able to increase soil elevation (Langley et al. 2009; McLeod et al. 2011; Kirwan and Megonigal 2013), a response controlled by a complex interaction of geological, hydrological and biological controls including sediment in-flow, tidal range, root biomass, litter production, etc. (Langley et al. 2009; McKee et al. 2012).

The increased frequency and intensity of storm events predicted with climate change also pose a threat to wetland C storage, as evidenced by peat collapse caused by storm-induced mortality in both mangroves and salt marshes (Cahoon et al. 2003; Cahoon 2006). As a result, the responses of coastal wetlands to future climate change, and especially the impacts to C storage, remain highly uncertain.

Mangrove range expansion poses a potential negative feedback to global warming where increases to mangrove extent will cause an increased uptake of atmospheric C, which could slow further warming. Though, as indicated above, the magnitude of this feedback is difficult to quantify. Current earth system models rely on global mangrove distributions mapped at spatial resolutions too coarse (30 m) to distinguish encroaching mangroves from marshes (Giri et al. 2011b), and as currently parameterized, may not adequately account for the potential feedbacks to global C storage and cycling caused by a broad scale mangrove range shift (Alongi 2014; Bouillon et al. 2008). Our findings that rapid vegetation shifts can cause dramatic increases in wetland C sequestration have implications for the role of blue carbon and the C sink capacity of coastal wetlands along the Atlantic seaboard and across North America.

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