

Salt marsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools

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Summary

1. Changing winter climate extremes are expected to result in the poleward migration of mangrove forests at the expense of salt marshes. Although mangroves and marshes are both highly valued ecosystems, the ecological implications of mangrove expansion have not been fully investigated.

2. Here, we examined the effects of mangrove expansion on below-ground properties related to peat development and carbon storage. We investigated plant–soil interactions in marshes and across mangrove forest structural gradients in three locations in the northern Gulf of Mexico (USA). We compared our results to those from terrestrial grasslands where the effects of woody plant encroachment are often influenced by rainfall and plant traits.

3. Abiotic conditions at our study locations differed, particularly in terms of physicochemical properties related to precipitation. Marsh species composition, marsh above-ground biomass, and mangrove forest structural complexity also varied across these locations. Marshes in the driest location (Central Texas) had higher salinities and were dominated by low biomass succulent plants and lower soil carbon pools. Marshes in the wetter, less saline locations (Louisiana and North Florida) contained high biomass grasses and higher soil carbon pools.

4. At all locations, above-ground biomass and above-ground carbon pools were higher in mangroves than marshes; however, below-ground soil carbon pools were only higher in mangroves than marshes in the driest location. In the wetter locations, the linkages between mangrove forest structure and soil properties were minimal or not significant. However, in the driest location, there was a significant increase in soil properties related to peat development and carbon storage with increased mangrove forest structural development.

5. Synthesis: Our results indicate that the ecological implications of woody plant encroachment in tidal saline wetlands are dependent upon precipitation controls of plant–soil interactions. Although the above-ground effects of mangrove expansion are consistently large, below-ground influences of mangrove expansion appear to be greatest along low-rainfall coasts where salinities are high and marshes being replaced are carbon poor and dominated by succulent plants. Collectively, these findings complement those from terrestrial ecosystems and reinforce the importance of considering rainfall and plant–soil interactions within predictions of the ecological effects of woody plant encroachment.

Key-words: carbon storage, climate change, ecotone, forest development, mangrove forest, plant–soil (below-ground) interactions, range expansion, salt marsh, soil development, woody plant encroachment

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Introduction

In tidal saline wetlands, changing winter air temperature extremes are expected to result in the poleward expansion of mangrove forests at the expense of salt marshes (Osland *et al.* 2013; Cavanaugh *et al.* 2014; Saintilan *et al.* 2014; Alongi 2015). Mangroves are unable to survive severe or prolonged freeze events; hence, the latitudinal limit of mangrove forests is largely determined by winter temperature extremes. In the wet tropics and subtropics, tidal saline wetlands are dominated by mangrove trees. In contrast, tidal saline wetlands in temperate climatic zones are dominated by salt marsh graminoid and succulent plants (West 1977; McKee, Rogers & Saintilan 2012). Where salt marshes and mangrove forests meet in the temperate-tropical climatic transition zone, they form an ecotone between the two ecosystems. This ecotonal boundary consists of a dynamic mosaic of salt marsh and mangrove forest patches that is greatly influenced by the frequency and intensity of winter temperature extremes (Osland *et al.* 2015, 2016).

In addition to providing fish and wildlife habitat, mangrove forests and salt marshes protect coastlines from erosion, improve water quality, maintain coastal food webs, and attenuate waves (Barbier *et al.* 2013). Mangrove forests and salt marshes are both highly valued ecosystems, but the ecological implications associated with mangrove forest expansion at the expense of salt marsh have not been fully investigated. Here, we provide a foundation for such understanding by focusing on the effects of mangrove forest expansion and forest development upon above- and below-ground ecosystem properties related to peat development and carbon storage. Due to high primary productivity and slow microbial decomposition, salt marshes and mangrove forests both maintain soil carbon stocks and burial rates that are typically greater than their terrestrial grassland and forest counterparts (Chmura *et al.* 2003;

Donato *et al.* 2011; McLeod *et al.* 2011). In restored, created, and recently formed mangrove forests, soil peat development often occurs rapidly and concurrently with forest growth and development (Alongi 2009; Lovelock *et al.* 2010; Osland *et al.* 2012). Based upon this knowledge, we hypothesized that, in multiple locations, there would be a positive relationship between mangrove forest structure and soil properties related to peat development and carbon storage (see illustration of this hypothesis in Fig. 1a–c). We also expected that soil properties present in mangroves would differ from those present in nearby salt marshes.

In many dryland ecosystems, woody plant encroachment results in an increase in above- and below-ground resources (i.e., higher carbon and nitrogen pools) (Schlesinger *et al.* 1990; Throop & Archer 2008; Eldridge *et al.* 2011). However, the effects of woody plant encroachment on ecosystem structure and function are often location dependent and greatly influenced by rainfall-plant trait interactions (Knapp *et al.* 2008; Maestre *et al.* 2009). The middle panels of Fig. 1 represent a hypothesis where a positive plant–soil relationship is present in certain locations (e.g., Fig. 1d) but not in others (e.g., Fig. 1e,f). This alternative hypothesis fits well with results from terrestrial grasslands where woody plant encroachment has resulted in higher soil carbon pools in areas with low rainfall but not in areas with high rainfall (Jackson *et al.* 2002; Eldridge *et al.* 2011). The lower panels of Fig. 1 (g–i) represent an alternative hypothesis where, in all locations, there are no positive plant–soil relationships and no below-ground differences between salt marshes and mangroves.

Our investigation was conducted along the northern Gulf of Mexico coast, where the effects of climate change-induced mangrove forest expansion into salt marsh are expected to be especially large (Montagna *et al.* 2011; Osland *et al.* 2013, 2015, 2016). To our knowledge, there are only four published

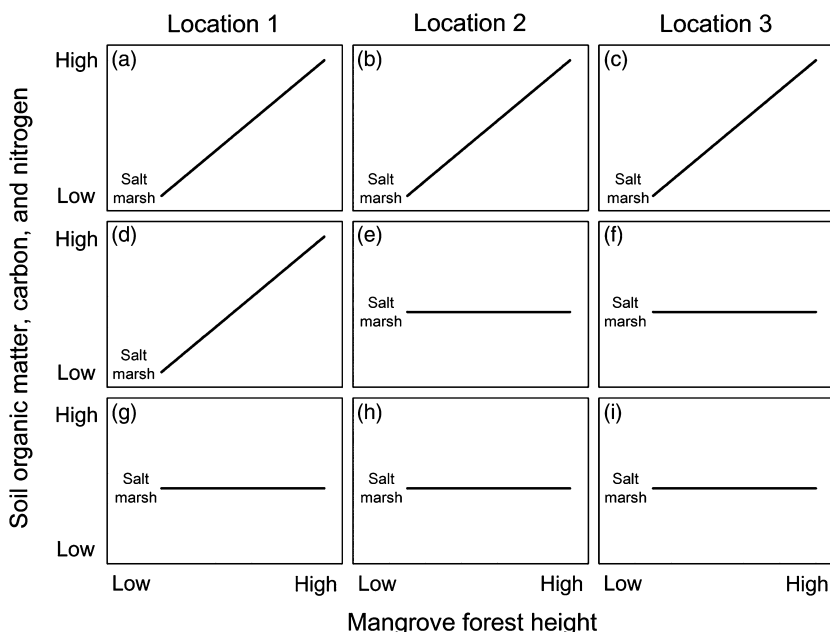


Fig. 1. An illustration of various hypotheses regarding plant–soil relationships across mangrove forest structural gradients in different locations: (a–c) a positive plant–soil relationship in multiple locations, (d–f) a positive plant–soil relationship in certain locations but not in others, (g–i) there is not a positive plant–soil relationship in any location. Although the positive relationships depicted here are linear, nonlinear plant–soil relationships across mangrove forest structural gradients are also possible (e.g., Osland *et al.* 2012).

studies that have investigated the below-ground effects of mangrove forest expansion in the northern Gulf of Mexico (Perry & Mendelssohn 2009; Comeaux, Allison & Bianchi 2012; Bianchi *et al.* 2013; Henry & Twilley 2013), and all four of these studies were conducted in low-stature mangrove forests. In a recent study conducted on the Atlantic coast of Florida, (Doughty *et al.* 2016) reported that although mangrove forest expansion and replacement of salt marsh resulted in greater above-ground carbon pools, there was no effect of mangrove expansion upon soil carbon pools. Of the existing North American studies, the only studies to have identified a positive effect of mangrove expansion on soil properties, including soil carbon stocks, were conducted in succulent dominated marshes with low precipitation in Texas (Comeaux, Allison & Bianchi 2012; Bianchi *et al.* 2013).

Our study provides a foundation for addressing the following questions: (i) How do above- and below-ground ecosystem properties differ between salt marshes and mangrove forests; (ii) What are the effects of mangrove forest encroachment into salt marsh upon soil development, especially peat formation and carbon and nitrogen storage; and (iii) How do plant–soil interactions across mangrove forest structural gradients vary in different abiotic settings, including areas with differing rainfall regimes and differing salt marsh plant communities? To address these questions, we utilized salt marshes and the natural black mangrove (*Avicennia germinans*) forest structural gradients present at three discrete locations in the northern Gulf of Mexico: Cedar Key (North Florida), Port Fourchon (Louisiana), and Port Aransas (Central Texas). Each of these three locations represents a distinct combination of climate-driven abiotic conditions that govern plant traits and plant–soil interactions. Rainfall is much lower at the Central Texas location than the Louisiana and North Florida locations. As a result, marshes in the Central Texas location have higher salinities and are generally dominated by succulent plants with lower above-ground biomass and lower soil carbon pools. In contrast, marshes in the wetter locations (Louisiana and North Florida) have higher above-ground

biomass, contain grasses, and have higher soil carbon pools. These contrasting conditions enable us to provide insights into how rainfall controls of plant–soil interactions may affect the ecological implications of mangrove forest encroachment into salt marsh. At all three locations, we quantified relationships between plant community composition and structure, soil and porewater physicochemical properties, tidal inundation and climatic conditions.

Materials and methods

STUDY AREA

We selected three distinct locations within the salt marsh-mangrove ecotone in the northern Gulf of Mexico where *A. germinans* individuals exist at their latitudinal limit (Fig. 2). The three locations were near Port Aransas, Texas (hereafter Central Texas; 27.854°–27.912° N, 97.055°–97.072°W), Port Fourchon, Louisiana (hereafter Louisiana; 29.100°–29.110°N, 90.193°–90.201°W), and Cedar Key, Florida (hereafter North Florida; 29.141°–29.143°N, 83.021°–83.032°W). The Central Texas location is a relatively dry area (mean annual precipitation: 900 mm) with a 30-year minimum air temperature of –9.7 °C. The Louisiana location has a 30-year minimum air temperature of –9.7 °C and is located in the historical Mississippi River Delta with a mean annual precipitation at 1580 mm. Finally, the North Florida location has a mean annual precipitation of 1270 mm and a 30-year minimum air temperature of –9.5 °C. All three locations are micro-tidal environments; Louisiana and Central Texas have mean tidal ranges of 0.37 and 0.27 m, respectively, and North Florida has a larger mean tidal range of 0.86 m (NOAA, 2014a,b; TCOON, 2014, respectively). *Avicennia germinans* is the dominant mangrove species in all three locations. The salt marsh vegetation in the Louisiana, North Florida and Central Texas locations is dominated by solely halophytic grasses, a mixture of grasses and succulent forbs, and solely succulent forbs, respectively.

EXPERIMENTAL DESIGN

At each of the three locations, three salt marsh and nine mangrove sites were identified (i.e., 12 sites per location; three locations; 36 total



Fig. 2. Map of the three sampling locations for this study: Port Aransas, Texas (Central Texas), Port Fourchon, Louisiana (Louisiana) and Cedar Key Florida (North Florida).

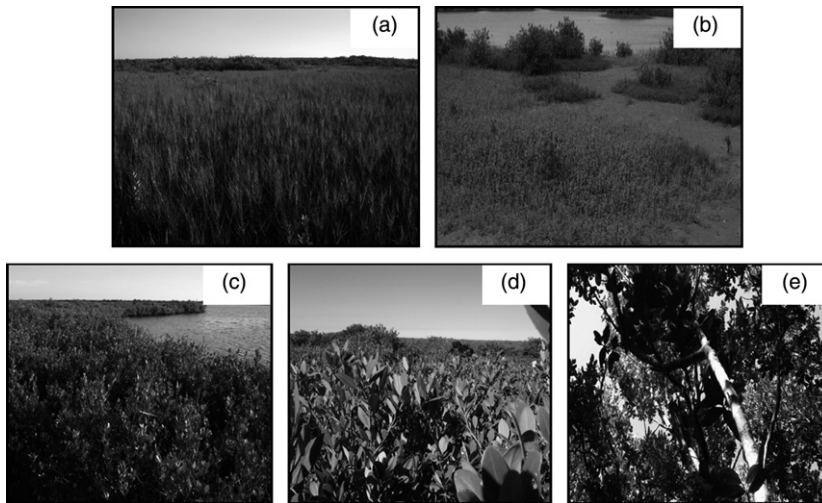


Fig. 3. Photos of salt marsh sites (a and b) and mangrove forest sites (c, d and e). The mangrove photos depict a forest structural gradient that extends from short to tall (c to e, respectively). Note that whereas the marsh in Louisiana is grass-dominated, the marsh in Central Texas is succulent plant-dominated (a and b, respectively). The mangrove forest photos (c, d and e) are from Louisiana, Central Texas and North Florida, respectively.

sites). The nine mangrove sites spanned the natural *A. germinans* structural gradient present within each location and captured varying stages of forest development (Fig. 3). Mangrove sites were selected to represent uniform size classes that were defined primarily by height to capture the mangrove structural gradient. A similarity in elevation was also a criterion for selecting sites. The three salt marsh sites within each location were dominated primarily by salt marsh species. Please note that our structural gradient experimental approach is not necessarily indicative of age. We did not have enough historical information about these sites to use an age-based chronosequence approach, and while forest height can be indicative of age in some settings, mangrove forest height is also greatly influenced by abiotic factors (Day *et al.* 1987; Méndez-Alonzo, López-Portillo & Rivera-Monroy 2008; Ross *et al.* 2009). In general, a tall mangrove forest is indicative of a combination of enough time without disturbance (e.g., time without freeze events, hurricanes) as well as suitable abiotic conditions that allow growth to occur (e.g., appropriate nutrient, freshwater, salinity, hydrological regimes). Warmer winter temperature regimes are expected to lead to taller mangrove forests in these study areas due to: (i) more time without damaging freeze events; and (ii) higher growth rates in response to warmer temperatures and a longer growing season.

At each site, we established one 100-m² circular plot (radius: 5.65 m), and all measurements were collected from within this 100-m² plot. Sampling in ecosystems with high structural diversity and multiple morphologies of mangrove trees, shrubs, and salt marshes can be challenging, and in this study we used a sampling design that included multiple strata and a series of nested subplots (*sensu* Osland *et al.* 2012). Within the 100-m² circular plot, we randomly established three nested 1-m² subplots and three 0.25-m² subplots for determination of small-scale characteristics (e.g., herbaceous layer, soil, and porewater properties), using a randomly assigned compass direction and distance from the centre of the plot. Larger subplots (e.g., 2, 25 m²) were also established on a density-dependent basis to adequately characterize some mangrove forest structural properties (e.g., short tree strata), which occurred at variable densities.

HYDROLOGY, ELEVATION AND CLIMATE

We calculated the percentage of time the soil surface was flooded (hereafter percent time flooded) by determining plot elevations and relating these to local hydrological regimes (i.e., tidal data). Elevation was determined for the centre of each plot via real time kinematic survey (RTK) (Trimble R8 Receiver & Trimble TSC3 Controller,

Trimble Navigation, Ltd., Sunnyvale, CA, USA), and expressed in North American Vertical Datum of 1988 (NAVD88) Geoid 12A. Local tide gauges were utilized to determine hourly water level data from 5 years prior to March 2013 for each location (Cedar Key, Florida- NOAA [National Oceanic and Atmospheric Administration] Tides and Currents-Station ID: 8727520; Port Fourchon, Louisiana-CRMS [Coastal Reference Monitoring System]-Station ID: CRMS0292; Port Aransas, Texas-TCOON [Texas Coastal Ocean Observation Network]-Station ID: DNR-009). All water levels were either collected in, or converted to, NAVD88-Geoid 12A to be directly comparable with survey measurements to determine percent time flooded. Due to high rates of subsidence, the Port Fourchon, Louisiana, tidal data from the CRMS database was corrected for gauge subsidence prior to being converted into NAVD88-Geoid 12A. Extreme minimum air temperature and mean annual precipitation for each of the three locations were determined from gridded observed climate data sets produced by the PRISM Climate Group using the Parameter-elevation Relationships on Independent Slopes (PRISM) (Daly *et al.* 2008) for the time period 1981–2010. The resolution of the air temperature and precipitation data used were 2.5 arc-min (~4-km cells) and 30 arc-s (~1-km cells), respectively. The minimum temperature data were determined from daily data and represent the absolute coldest air temperature for each location recorded during that period. For the Gulf of Mexico coast, the 1981–2010 time period is appropriate for characterizing extreme winter air temperature events since it captures the extreme winter events that occurred in the 1980s (i.e., the freeze events of 1982, 1983, 1985 and 1989).

SOIL

Within each 100-m² plot, soil cores were collected to a depth of 30 cm from a 1-m buffer surrounding each of the three 1-m² subplots. Each of these three cores was partitioned into depth increments of 0–5, 5–15 and 15–30 cm from the soil surface and then composited by depth increment in the field. We expected that any mangrove expansion-induced effects on soil properties would be most evident in the upper soil layers (0–5, 5–15 cm), and less evident in the lowest layer (Mitsch & Gosselink 2000; Lovelock *et al.* 2010; Osland *et al.* 2012). A set of another three cores was similarly collected, partitioned by depth, and composited for a sample that was dedicated solely for the determination of bulk density and soil moisture. The coring device used to collect soil samples was a custom-made stainless steel split corer (4.7-cm diameter, split cylinder with a piano hinge)

(Osland *et al.* 2012). Samples were kept cool until processing. Soil cores for physicochemical analyses were dried at 60 °C, homogenized with a mortar and pestle, and sieved through a 2-mm screen prior to all analyses. Subsamples for elemental analyses were homogenized using a planetary mill (Frisch Pulviresette, New York, NY, USA). An elemental analyser (Flash EA 1112, NC Soils, Thermo Quest, Thermo Fisher Scientific, Waltham, MA, USA) was used to measure Total Nitrogen (TN) and Total Carbon (TC) via dry combustion (McGill & Figueiredo 1993; Tiessen & Moir 1993; respectively). TN and TC were converted from percentages to grams per m² and megagrams (Mg) per hectare, respectively, based on bulk density measurements and the area of the sampling device. This was performed to facilitate comparisons of the three locations, as their soil properties differed substantially. Soil organic matter (SOM) was determined via loss on ignition in a muffle furnace at 475 °C for 16 h (Wang, Li & Wang 2011). Bulk density samples were dried at 105 °C to a constant mass and simple dry weight to volume ratios were used to calculate bulk density (Blake & Hartge 1986). Percent soil moisture was determined via the weight difference after drying.

POREWATER

Within each 100-m² plot, porewater samples were collected with a siphon tube apparatus (McKee, Mendelsohn & Hester 1988) from each of the three 1-m² subplots at a depth of 15 cm below the soil surface. In situ determinations of salinity were completed in the field using a hand-held meter (YSI 30, YSI Inc., Yellow Springs, OH, USA).

VEGETATION

A variety of vegetation measurements at multiple strata were performed to capture differences in vegetation structure. Within the 100-m² plots, three broad categories were utilized for all measurements: tall tree mangroves (>1.4 m in height), short tree mangroves (0.3–1.4 m in height), and salt marsh species. Percent cover was visually estimated for each of three strata, as well as an integrated total, which was an estimate of percent cover for the entire plot regardless of strata and did not exceed 100%. Measurements of mangrove individuals were divided into the two different strata (i.e., tall trees and short trees). For the short tree stratum, we measured total height, basal diameter (stem diameter at 0.3 m above the soil surface), and perpendicular crown diameters (*sensu* Osland *et al.* 2014a). Since our sites were selected to capture structural gradients, the structural complexity and diversity of the vegetation at our sites was high (i.e., sites that ranged from marsh to dense shrubs to tall forests). As a result, the density of short trees and tall trees was highly variable. Depending upon the density of the short tree stratum, measurements were performed in either the whole plot or an appropriate subdivision that enabled approximately 20 individuals to be included. Most often the short tree measurements were recorded within two nested and randomly located 2-m² subplots. Similarly, height and diameter at breast height (DBH: defined as at 1.4 m above the soil surface) of tall trees was determined in the whole plot or a subplot that enabled approximately 20 individuals to be included. Above-ground biomass for the short tree stratum was estimated via an allometric equation for freeze-affected *A. germinans* individuals that utilizes plant volume measurements (i.e., a combination of crown diameter and plant height measurements) (Osland *et al.* 2014a). Above-ground biomass for tall trees was estimated using a species-specific allometric equation that utilizes DBH (Smith & Whelan 2006). Total estimated above-ground mangrove biomass was used to estimate grams of carbon per m² and also

megagrams of carbon per hectare by utilizing a 41.5% conversion (Bouillon *et al.* 2008).

Salt marsh plant cover and canopy height was estimated within all 1-m² subplots, and species-specific stem density, pneumatophore density, and pneumatophore height were determined within each of the nested 0.25-m² subplots. To determine marsh biomass and estimate above-ground carbon stocks, clip plots from all three of the 0.25-m² subplots were harvested once near the end of the growing season and combined into a composite sample for each site. Upon returning to the lab, clip plot samples were sorted by species into live and dead components, dried at 60 °C, and dry weight was recorded. Stem density and shoot height were determined for each herbaceous species. Total above-ground salt marsh biomass was used to estimate grams of carbon per m² and also megagrams of carbon per hectare by utilizing a 44.0% conversion (McKee & Rooth 2008).

DATA ANALYSES

Prior to all analyses, the subplot-level data were converted to site-level data via calculation of site-level means and/or normalization of subplot data to site-wide areal extents. Our first series of models included data from all three locations. For the elevation, hydrologic, porewater, vegetation and soil variables, we evaluated two-way analysis of variance (ANOVA) models that included the following independent variables: location (Central Texas, Louisiana, North Florida), habitat type (mangrove and salt marsh) and their interaction. Although our data exhibited mild departures from normality and homogeneity of variance in certain cases, ANOVA is generally regarded as robust in respect to minor violations of these assumptions (Neter *et al.* 1996). Depth was not included in the first statistical models as the majority of the significant findings were between locations and depth was further examined within each location. Following these cross-location comparisons, we evaluated location-specific models that were focused on soil physicochemical properties. For soil properties within each location, we evaluated two-way ANOVAs that included the following dependent variables: habitat type, depth and their interaction. Also within each location and for soil properties present within an individual soil depth increment, we evaluated analysis of covariance (ANCOVA) models that included the following independent variables: habitat, elevation and mean mangrove height. Elevation was included as a covariate in these latter models to account for any potential confounding influence of this important abiotic variable. Post hoc mean comparisons were conducted using Tukey's HSD tests. Bivariate linear regression was utilized to quantify the relationships between above- and below-ground properties within mangrove forests at each of the three locations. To illustrate the multivariate relationships between above- and below-ground ecosystem properties, we conducted two separate principal components analyses (PCAs) for each location, one PCA for soil properties (0–30 cm) and one PCA for vegetation properties within each location. We used linear regression to quantify the relationships between the soil and vegetation principal component axes. PCA site scores were used to depict the location of individual sites in multivariate soil and vegetation space. All statistical analyses were completed in JMP Pro 11 (SAS Institute Inc., Cary, NC, USA).

Results

ELEVATION AND HYDROLOGY

Elevation and percent time flooded differed significantly by location (Elevation: $F_{2,35} = 52.4$, $P < 0.001$; Flooding:

$F_{2,35} = 32.1$, $P < 0.001$), habitat (Elevation: $F_{1,35} = 5.3$, $P < 0.05$; % Time Flooded: $F_{1,35} = 5.1$, $P < 0.05$), and their interaction (Elevation: $F_{2,35} = 4.0$, $P < 0.001$; % Time Flooded: $F_{2,35} = 11.3$, $P < 0.001$). Of the three locations, the North Florida sites were highest in elevation and inundated the least frequently (Table 1). Central Texas sites were intermediate in elevation and Louisiana sites were the lowest in elevation (Table 1). Louisiana and Central Texas sites had greater percent time flooded than North Florida and did not significantly differ from one another (Table 1). Within North Florida and Central Texas, there was no significant difference in elevation or percent time flooded between the mangrove and salt marsh sites (Table 1). In Louisiana, the salt marsh sites were slightly lower in elevation and more frequently flooded than the mangrove sites (Table 1).

POREWATER

Porewater salinity differed significantly by location ($F_{2,34} = 15.4$, $P < 0.001$), but not by habitat or their interaction (Table 1). Salinity was greatest in Texas compared to both Louisiana and North Florida (Table 1).

VEGETATION

Salt marsh vegetation metrics differed significantly by location (Salt Marsh Biomass: $F_{2,35} = 94.2$, $P < 0.001$; Grass Biomass: $F_{2,35} = 338.0$, $P < 0.001$; Salt Marsh Carbon: $F_{2,35} = 94.2$, $P < 0.001$). The Central Texas salt marsh sites were dominated by succulent species (*Batis maritima* and *Salicornia* spp.), whereas the Louisiana salt marsh sites were dominated by a grass species (*Spartina alterniflora*). The North Florida salt marsh sites contained a mixture of grass and succulent species (*S. alterniflora*, *B. maritima*, *Paspalum vaginatum* and *Salicornia* spp.) (Fig. 4a; Table S1 in Supporting Information). Total above-ground salt marsh biomass (i.e., grasses plus succulents), grass biomass, and salt marsh carbon stocks at salt marsh sites were highest in Louisiana, intermediate in North Florida, and lowest in Central Texas (Fig. 4a; Tables 1 and S2).

Mangrove vegetation metrics differed significantly by location (Mangrove Biomass: $F_{2,35} = 3.4$, $P < 0.05$; Mean Mangrove Tree Height: $F_{2,35} = 6.7$, $P < 0.01$; Mangrove Carbon: $F_{2,35} = 3.4$, $P < 0.05$). For the mangrove sites, mangrove forest structural attributes (i.e., mean tree height, total tree biomass, total mangrove above-ground carbon stocks) were higher in North Florida than in Central Texas or Louisiana (Figs 4b and 5; Tables 1, S2 and S3). Tree heights for the tallest single individual within each location were 9.1, 4.2 and 3.4 m for North Florida, Louisiana and Central Texas, respectively. Mean tree heights within North Florida, Louisiana and Central Texas location were 4.1 ± 0.5 , 1.4 ± 0.3 , and 1.3 ± 0.2 m, respectively. In North Florida, Louisiana and Central Texas, mangrove sites spanned a mean tree height gradient that ranged from 2.2 to 6.5, 0.5 to 2.7 and 0.4 to 2.1 m, respectively (Fig. 5).

SOIL AND PLANT–SOIL INTERACTIONS

Soil properties differed between the three locations (TC: $F_{2,35} = 63.0$, $P < 0.001$; TN: $F_{2,35} = 111.2$, $P < 0.001$; SOM: $F_{2,35} = 317.0$, $P < 0.001$; BD: $F_{2,35} = 160.3$, $P < 0.001$; Soil Moisture: $F_{2,35} = 124.7$, $P < 0.001$). The soils at the North Florida sites had characteristics that were most indicative of peat development (i.e., lowest BD, highest SOM, highest mass-based TC and highest mass-based TN) (Figs 5 and 6; Tables 1 and S4). For all these characteristics (i.e., BD, SOM, mass-based TC and mass-based TN), the Louisiana sites were intermediate and the Central Texas sites had characteristics that were least indicative of peat development and more characteristic of mineral soils (i.e., highest BD, lowest SOM, lowest mass-based TC, low soil moisture and lowest mass-based TN) (Figs 5 and 6; Tables 1 and S4). Within locations, the effects of habitat, soil depth and their interaction were variable (Figs 5 and 6; Tables 1, S4 and S5). Within Louisiana and North Florida, the interaction between habitat and depth was not significant for all of the soil variables that we measured, and the effect of habitat was only significant for TC in Louisiana (Figs 5 and 6; Tables 1, S4 and S5). Whereas the effect of soil depth in North Florida was significant for most soil variables, the effect of soil depth in Louisiana was significant for TC and TN (Figs 5 and 6; Tables 1, S4 and S5). In contrast, the effects of habitat, depth, and their interaction in Central Texas were significant for many soil variables (Figs 5 and 6; Tables 1, S4 and S5). In Central Texas, ANCOVA results indicated a significant relationship between increasing mangrove tree height and various soil properties (i.e., SOM (positive), TC (positive), TN (positive), BD (negative)) in many of the upper soil depth increments (i.e., 0–5 and 5–15-cm depth), but typically not in the lowest soil depth increment (15–30 cm depth), after accounting for the influence of elevation (Fig. 5, Table 1 and S6). In contrast, mangrove tree height in Louisiana and North Florida did not have an effect on most soil properties regardless of depth (Table S6). Linear regression models between mean mangrove tree height and SOM and soil TC support the presence of a positive plant–soil interaction in Central Texas, but not in Louisiana or North Florida (Fig. 5). While there was a significant positive relationship between mean mangrove tree height and SOM and soil TC at some soil depth increments in Central Texas, this relationship was not present in North Florida or Louisiana at any soil depth increments (Fig. 5; Tables 1 and S6).

The PCA results depict the multivariate position of individual sites in vegetation and soil space (the horizontal and vertical axes, respectively; Fig. 6; Tables S7 and S8). These analyses highlight and reinforce the influence of plant–soil interactions (i.e., a relationship between soil properties and mangrove forest structure) in Central Texas and the lack of a plant–soil interaction in the Louisiana and North Florida sites. Within each of these locations, the Vegetation PCA along the horizontal axis accounts for much of the variation in plant community structural attributes across the salt marsh sites and the mangrove forest structural gradient (Central Texas:

Table 1. Hydrology, porewater, above-ground carbon, and select soil properties (Mean \pm SE) within salt marsh and mangrove forests at each location. Different letters represent significant differences between locations and habitat types. Soil properties include depth in addition to location and habitat and show significant differences between habitat types and depths within each location and are denoted with different letters

Location	Hydrology (2008–2013)										Above-ground Carbon			Soil Properties		
	Habitat	Depth (cm)	Elevation (m) (NAVD88-Geoid 12A)	Time flooded (%)	Porewater		Salt marsh		Mangrove		Bulk density (g cm ⁻³)	Soil Moisture (%)	Soil Nitrogen (mg cm ⁻³)			
					Salinity (ppt)	0 ^C	0.01 \pm 0.01 ^C	0.01 \pm 0.01 ^C	0.01 \pm 0.004 ^B							
North Florida	Mangrove	0–5	0.49 \pm 0.05 ^A	11.5 \pm 2.0 ^P	33.2 \pm 1.6 ^B	0 ^C	63.87 \pm 13.27 ^A	0.19 \pm 0.01 ^B	66 \pm 2 ^A	2.0 \pm 0.1 ^A						
		5–15						0.25 \pm 0.01 ^{AB}	65 \pm 2 ^A	2.3 \pm 0.1 ^A						
	Salt marsh	15–30	0.41 \pm 0.01 ^{AB}	15.2 \pm 0.4 ^{CD}	28.6 \pm 0.04 ^B	2.36 \pm 0.56 ^B	0.01 \pm 0.01 ^B	0.29 \pm 0.02 ^A	60 \pm 3 ^A	2.0 \pm 0.1 ^A						
		0–5						0.16 \pm 0.02 ^B	69 \pm 3 ^A	1.9 \pm 0.2 ^A						
		5–15						0.23 \pm 0.02 ^{AB}	69 \pm 3 ^A	2.4 \pm 0.03 ^A						
		15–30						0.32 \pm 0.06 ^A	59 \pm 10 ^A	2.0 \pm 0.3 ^A						
Louisiana	Mangrove	0–5	0.11 \pm 0.02 ^C	33.8 \pm 4.4 ^{BC}	41.5 \pm 2.6 ^B	0 ^C	14.76 \pm 3.98 ^B	0.43 \pm 0.03 ^A	57 \pm 2 ^A	1.3 \pm 0.1 ^{AB}						
		5–15						0.54 \pm 0.04 ^A	56 \pm 2 ^A	1.7 \pm 0.1 ^A						
	Salt marsh	15–30	-0.09 \pm 0.07 ^D	66.6 \pm 11.9 ^A	29.6 \pm 2.2 ^B	3.4 \pm 0.08 ^A	0.01 \pm 0.004 ^B	0.57 \pm 0.06 ^A	57 \pm 2 ^A	1.3 \pm 0.1 ^{AB}						
		0–5						0.39 \pm 0.05 ^A	60 \pm 3 ^A	1.1 \pm 0.3 ^{AB}						
		5–15						0.6 \pm 0.24 ^A	61 \pm 6 ^A	1.5 \pm 0.4 ^{AB}						
		15–30						0.31 \pm 0.03 ^A	66 \pm 4 ^A	1.0 \pm 0.3 ^B						
Central Texas	Mangrove	0–5	0.25 \pm 0.01 ^B	42.1 \pm 2.2 ^B	48.2 \pm 3.3 ^A	0.01 \pm 0.01 ^C	13.05 \pm 5.84 ^B	0.64 \pm 0.05 ^C	51 \pm 3 ^A	1.3 \pm 0.1 ^A						
		5–15						0.93 \pm 0.07 ^B	38 \pm 2 ^B	0.7 \pm 0.1 ^B						
	Salt marsh	15–30	0.29 \pm 0.01 ^{BC}	31.4 \pm 2.1 ^{BCD}	51.9 \pm 6.2 ^A	0.11 \pm 0.09 ^C	0.59 \pm 0.25 ^B	1.20 \pm 0.04 ^A	29 \pm 1 ^C	0.4 \pm 0.1 ^C						
		0–5						1.15 \pm 0.05 ^{AB}	28 \pm 1 ^{BC}	0.6 \pm 0.1 ^{BC}						
		5–15						1.33 \pm 0.04 ^A	25 \pm 1 ^C	0.4 \pm 0.03 ^{BC}						
		15–30						1.39 \pm 0.04 ^A	24 \pm 1 ^C	0.2 \pm 0.02 ^B						

Correction added after online publication on 19 April 2016: units for Above-ground Carbon changed to Mg ha⁻¹ and units for Bulk density changed to g cm⁻³

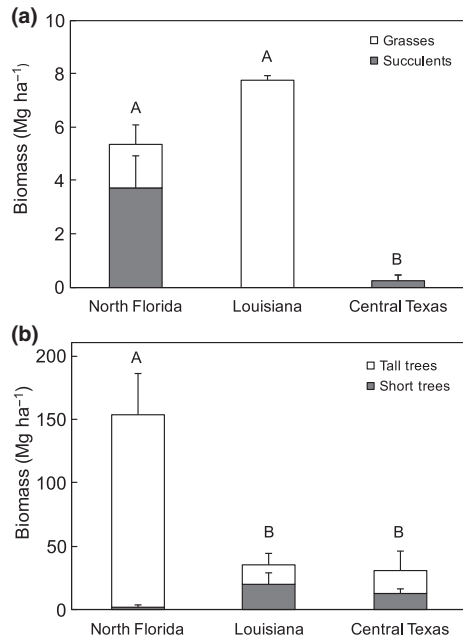


Fig. 4. Above-ground biomass (Mean \pm SE) of salt marshes (a) and mangrove forests (b) within each location. Whereas the salt marsh biomass is separated into grass and succulent-plant categories, the mangrove forest biomass is separated into the Tall Tree and Short Tree strata. Different letters denote significant differences in total above-ground biomass between locations.

59.4%, Louisiana: 70.5%, North Florida: 79.7%). The Soil PCA along the vertical axis accounts for much of the variation in soil properties within each location (Central Texas: 94.7%, Louisiana: 62.6%, North Florida: 52.8%). Each of the axes depicted represents the single most important (i.e., highest proportion of variance accounted for) axis within their respective analyses. In North Florida and Louisiana, there was no relationship between the position of individual sites along the vegetation and soil PCAs (Fig. 6a,b). In contrast, there was a positive relationship between the soil and vegetation site scores in Central Texas (Fig. 6c). This finding was reinforced by analyses of the relationships between above-ground and soil carbon stocks within each location. In North Florida and Louisiana, there was no relationship between above-ground and soil carbon stocks; however, in Central Texas, there was a positive relationship between above-ground carbon stocks and soil carbon stocks ($R^2 = 0.67$).

Discussion

At global and regional scales, macroclimatic drivers greatly influence ecosystem structure and function in tidal saline wetlands by modulating abiotic conditions and governing the performance, abundance and interactions of foundation plant species (Guo *et al.* 2013; Osland *et al.* 2013; Osland, Enwright & Stagg 2014b). In tidal saline wetlands, foundation plant species (*sensu* Dayton 1972; Ellison *et al.* 2005) play an important functional role in that they create habitat, alter abiotic conditions, support ecological communities and

influence soil processes (Pennings & Bertness 2001; McKee, Cahoon & Feller 2007; Reddy & DeLaune 2008; Alongi 2009). Interactions between air temperature and rainfall regimes greatly determine whether a tidal saline wetland habitat will be dominated by mangrove trees, salt marsh graminoids, salt marsh succulents and/or algal mats (Adam 1990; Saenger 2002; Osland *et al.* 2016).

In our driest study location (Central Texas), salt marsh plant communities and soil carbon pools were much different than in the wetter locations (North Florida and Louisiana). In low-rainfall tidal saline wetland environments like those in Central Texas, hypersaline and physiologically stressful conditions are common as oceanic salts accumulate once tidal waters evaporate (Zedler 1980; Pulich & Rabalais 1986; Ridd, Sandstrom & Wolanski 1988). The halophytic plants found in these environments must be able to tolerate highly stressful and dynamic conditions. Indicators of salt marsh plant productivity and performance (e.g., plant height and biomass) were lower in the more saline Central Texas location than in the other two study locations. Plant community composition was also different in the Central Texas location, where the marshes were dominated solely by stress-tolerant succulent plant species rather than grasses (as in Louisiana) or a combination of grasses and succulent plants (as in North Florida).

Due to interactions between rainfall, salinity and plant physiology and performance, soil carbon pools in the drier and more saline Central Texas salt marshes were much lower than those present in the wetter and less saline Louisiana and North Florida salt marshes. In Louisiana and North Florida, the existing high soil carbon pools in the salt marsh sites are likely the product of high salt marsh plant productivity; that is, the high rates of salt marsh above-ground and below-ground net primary productivity have contributed to peat development and the high soil carbon and nitrogen pools observed. In contrast, low precipitation and high salinity at the Central Texas salt marsh sites likely constrain plant productivity and abundance (Zedler 1982; Alexander & Dunton 2002; Withers 2002; Osland, Enwright & Stagg 2014b), which limits the development of soil carbon and nitrogen pools.

In Central Texas, there was a positive relationship between mangrove forest above-ground structural development (e.g., tree height, above-ground biomass, above-ground carbon stocks) and indicators of peat development (e.g., higher soil carbon, nitrogen and organic matter; lower soil bulk density). In contrast, there was no variation in these indicators of peat development across the mangrove forest structural gradients in Louisiana and North Florida. These results indicate that, in tidal saline wetlands, the below-ground effects of woody plant encroachment are strongly linked to rainfall-salinity effects upon plant functional group abundance and performance. The below-ground effects of mangrove expansion are likely to be highest in drier climatic zones where pre-encroachment soil carbon pools are minimal due to low primary productivity of stress-adapted vegetation. In drier climates, soil carbon pools are likely to increase as mangrove forests expand into salt marsh and develop into forests. However, in wetter climatic

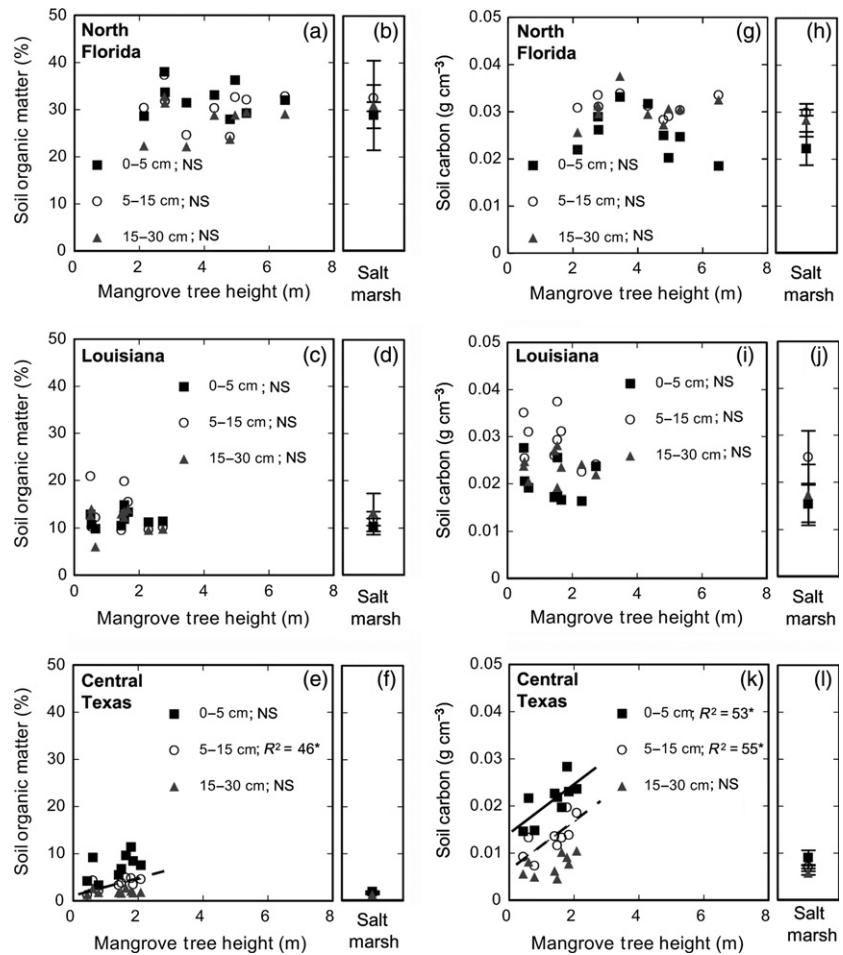


Fig. 5. (a, c, e): The relationship between mean mangrove tree height and soil organic matter at each location for each soil depth increment. (b, d, f): Soil organic matter (Mean \pm SE) at the salt marsh sites within each location for each soil depth increment. (g, i, k): The relationship between mean mangrove tree height and soil carbon at each location for each soil depth increment. (h, j, l): Soil carbon at the salt marsh sites within each location for each soil depth increment. Solid and dotted regression lines represent the 0–5 and 5–15 cm soil depth increments, respectively. * $P < 0.05$; NS, Not Significant

zones, mangrove forest encroachment into salt marsh may result in no overall change in bulk soil properties including soil carbon pools.

These location-dependent results provide context for both this and other related studies. While previous studies in Central Texas also found increased peat development and soil carbon storage with mangrove encroachment into salt marsh (e.g., Comeaux, Allison & Bianchi 2012; Bianchi *et al.* 2013), prior studies in Louisiana found no below-ground differences between mangrove forests and salt marshes (e.g., Perry & Mendelssohn 2009; Henry & Twilley 2014). The below-ground effects of mangrove expansion have not previously been investigated in the North Florida location. However, a study conducted about 100-km south near Tampa Bay (mean annual precipitation: 1176 mm) reported no differences in the bulk soil properties of mangroves and nearby marshes (Lewis, Brown & Jimenez 2014). On the Atlantic coast of Florida where rainfall is also comparatively high (mean annual precipitation: 1370 mm), Doughty *et al.* (2016) also found no soil carbon differences between mangrove forests and salt marshes.

In Australia, several recent studies have highlighted the importance of considering the environmental setting (e.g., position within the tidal frame, geomorphic position, proximity to freshwater and sediment inputs) as well as plant

community characteristics (e.g., mangrove forest vs. rush vs. succulent-dominated) when comparing edaphic properties of salt marshes and mangrove forests (Howe, Rodríguez & Saco 2009; Livesley & Andrusiak 2012; Lovelock *et al.* 2013; Saintilan *et al.* 2013; Kelleway *et al.* 2016). Across two 70-year chronosequences of continuous mangrove encroachment into succulent plant-dominated salt marshes in southeastern Australia (mean annual precipitation: 1084 and 1024 mm), mangrove encroachment resulted in higher above- and below-ground carbon stocks (Kelleway *et al.* 2016).

Collectively, these studies along with our findings show that the ecological effects of mangrove expansion and displacement of salt marsh are highly dependent upon the antecedent properties of the salt marsh ecosystem that is being displaced. Due to the high variability in salt marsh ecosystem structure and function across abiotic gradients (e.g., macroclimatic, salinity, geomorphic and flooding gradients) in the northern Gulf of Mexico and the rest of the world, the ecological implications of woody plant encroachment into salt marsh are variable and highly location-dependent. Our results indicate that the below-ground effects of woody plant encroachment into salt marshes are likely to be highest along low-rainfall coasts where hypersaline conditions are common and low-productivity succulent plants are most dominant within salt marshes.

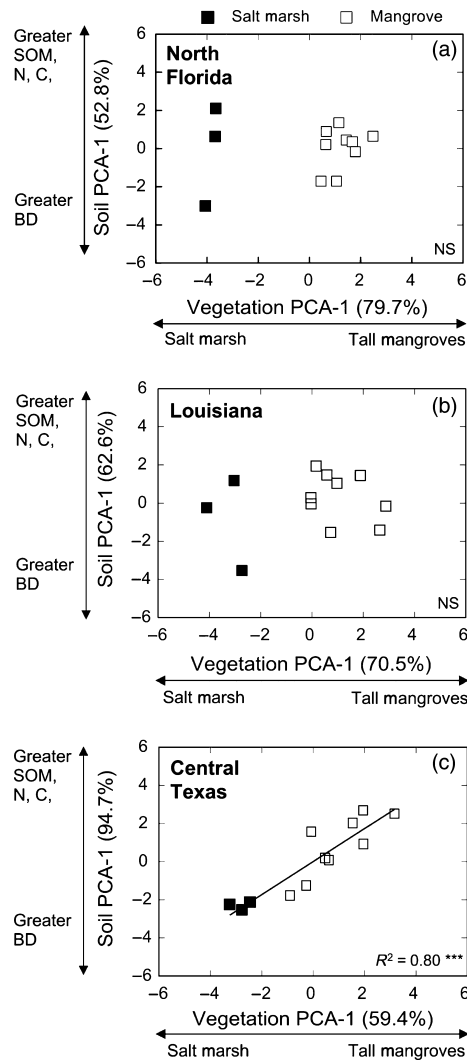


Fig. 6. The relationship between separate soil and vegetation principal component analyses (PCA) within each location (a, b, c). Whereas the horizontal axis (Vegetation PCA-1) represents the site score results for the vegetation PCA within each location, the vertical axis (Soil PCA-1) represents the site score results for the soil PCA within each location. Symbols represent individual site scores in multivariate soil and vegetation space. Linear regression of the site scores within each location was used to quantify plant–soil linkages. The text adjacent to each axis indicates the relationship between each PCA axis and the soil or vegetation variables. Soil property abbreviations are as follows: BD, Bulk Density; SOM, Soil Organic Matter; N, Soil Nitrogen; C, Soil Carbon; SM, Soil Moisture. *** $P < 0.001$, NS, Not Significant.

Although higher above-ground biomass and above-ground carbon pools are typically a product of woody plant encroachment into terrestrial grasslands, the effects upon below-ground soil properties are mixed (Knapp *et al.* 2008; Maestre *et al.* 2009; Eldridge *et al.* 2011). In arid and semi-arid terrestrial grasslands (i.e., where mean annual precipitation ≤ 850 mm), woody plant encroachment can result in lower soil pH, higher soil carbon and nitrogen pools, higher potential nitrogen mineralization, and higher levels of exchangeable calcium (Eldridge *et al.* 2011). In mesic terrestrial grasslands where above-ground net primary productivity is already relatively high due in part to high freshwater availability, woody plant

encroachment can result in a decrease (Jackson *et al.* 2002) or no net change (Briggs *et al.* 2005) in soil carbon and nitrogen pools. A recent comparison of the effects of afforestation of grasslands across a rainfall gradient produced similar results; soil carbon gains were observed in dry locations, while soil carbon losses were observed in wetter locations (Berthrong *et al.* 2012). In addition to rainfall regimes and abiotic conditions, plant traits can modulate the effects of encroachment on soil properties (Vitousek & Walker 1989; Maestre *et al.* 2009; Eldridge *et al.* 2011).

We live in a rapidly changing world where human-induced range expansions, non-native invasions and ecological regime shifts are becoming increasingly common (Vitousek *et al.* 1996; Scheffer *et al.* 2001; Parmesan & Yohe 2003). In terrestrial and wetland ecosystems, many of these regime shifts involve foundation plant species that are being replaced or lost (Ellison *et al.* 2005). Due to the importance of soil processes to ecosystem stability, structure and function, there is a pressing need to better understand the effects of these vegetation shifts on above-ground-below-ground interactions (Vitousek & Walker 1989; Wardle *et al.* 2004; Bardgett & Wardle 2010). Along subtropical coastlines across the globe, future changes in the intensity, duration and frequency of extreme freeze events are expected to result in the poleward migration of mangrove forests at the expense of some salt marsh ecosystems. Our results provide a foundation for better understanding the above-ground and below-ground effects of mangrove forest encroachment into salt marsh. Although the above-ground effects of mangrove encroachment are consistently large, the below-ground effects of mangrove encroachment appear to be greatest along low-rainfall coasts where salinities are high and the salt marshes being replaced are carbon poor and dominated by succulent plants. Collectively, these findings complement those from terrestrial ecosystems and reinforce the importance of considering rainfall controls of plant–soil interactions, particularly when predicting the ecological effects of woody plant encroachment.

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Data accessibility

All data for figures, tables, supplements and analysis can be found at: <https://www.sciencebase.gov/catalog/item/505b584be4b08c986b30c22d>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Salt marsh vegetation measurements (Mean \pm SE) within salt marsh and mangrove forests at each location. Significant differences between locations and habitat types are denoted with different letters.

Table S2. Above-ground biomass and carbon stocks (Mean \pm SE) within salt marsh and mangrove forests at each location. Significant differences between locations and habitat types are denoted with different letters.

Table S3. Mangrove vegetation measurements (Mean \pm SE) within salt marsh and mangrove forests at each location. Significant differences between locations and habitat types are denoted with different letters.

Table S4. Soil properties (Mean \pm SE) within salt marsh and mangrove forests at each location. Within each location, significant differences between habitat types and depths are denoted with different letters.

Table S5. Effect of habitat, depth, and their interaction on soil properties within each location.

Table S6. Effect of habitat, elevation, and mean mangrove height on soil properties at each depth within each location.

Table S7. Within locations the variable loadings for the most important axis for each vegetation Principal Component Analysis. For each location separate Principal Component Analysis were conducted for vegetation variables.

Table S8. Within locations the variable loadings for the most important axis for each soil Principal Component Analysis. For each location separate Principal Component Analysis were conducted for soil variables.