



Microspatial ecotone dynamics at a shifting range limit: plant–soil variation across salt marsh–mangrove interfaces

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Abstract

Ecotone dynamics and shifting range limits can be used to advance our understanding of the ecological implications of future range expansions in response to climate change. In the northern Gulf of Mexico, the salt marsh–mangrove ecotone is an area where range limits and ecotone dynamics can be studied in tandem as recent decreases in winter temperature extremes have allowed for mangrove expansion at the expense of salt marsh. In this study, we assessed aboveground and belowground plant–soil dynamics across the salt marsh–mangrove ecotone quantifying micro-spatial patterns in horizontal extent. Specifically, we studied vegetation and rooting dynamics of large and small trees, the impact of salt marshes (e.g. species and structure) on mangroves, and the influence of vegetation on soil properties along transects from underneath the mangrove canopy into the surrounding salt marsh. Vegetation and rooting dynamics differed in horizontal reach, and there was a positive relationship between mangrove tree height and rooting extent. We found that the horizontal expansion of mangrove roots into salt marsh extended up to eight meters beyond the aboveground boundary. Variation in vegetation structure and local hydrology appear to control mangrove seedling dynamics. Finally, soil carbon density and organic matter did not differ within locations across the salt marsh–mangrove interface. By studying aboveground and belowground variation across the ecotone, we can better predict the ecological effects of continued range expansion in response to climate change.

Keywords Coastal wetland · Plant community · Climate change · Carbon · Expansion dynamics

Introduction

Range limits and ecotones are two landscape features that are likely to respond to global climate change (Noble 1993; Walther et al. 2002; Parmesan and Yohe 2003; Van der Putten et al. 2010). Both features are constrained by abiotic, biotic, and dispersal limitations that define the expansion ability of a single species and/or an entire ecosystem (Gosz 1993; Peters et al. 2006; Van der Putten et al. 2010).

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These dynamic areas are sensitive to change and may serve as an appropriate proxy for future shifts, but only by understanding both aboveground and belowground processes are we able to fully comprehend current changes and new interactions.

Ecosystem transitions can be examined at a variety of scales to understand the factors that maintain their existence, define their shape, and control their advance and retreat (Gosz 1993; Peters et al. 2006). Ecotones, areas of transition between two ecosystems, form as a result of changes in biotic or abiotic drivers, such as climate, fire regime, herbivory, or other edaphic conditions (Risser 1995) with areas of overlap forming a mosaic (Watt 1947). Range limits are defined as the edges of a species' "ecological niche in space" (Sexton et al. 2009), with species only persisting in habitats and locations where they can tolerate conditions, successfully establish, and ultimately survive and reproduce. Analyses of range limits and ecotones are often difficult due to challenges in assessment and comparison, as temporal and spatial variability need to be considered (Fortin and Drapeau 1995; Fortin et al. 2000). Recently, a variety of spatial

detection analyses and curve fitting approaches have proven to be useful in beginning to understand, and more importantly compare, transitional patterns across range limits and ecotones (Fortin et al. 2000; Hufkens et al. 2008, 2009; Danz et al. 2013). Understanding these transitions of species and ecosystems is just as critical as understanding species range interiors and homogenous portions of each ecosystem (Lloyd et al. 2000) because landscapes and species distributions are naturally patchy and exist along a continuum (Breashers 2006). Species ranges and ecotonal transitions that respond quickly to changes in climate are valuable areas for monitoring climate change and advancing understanding of climate change impacts (Noble 1993).

The boundary between salt marsh and mangrove may be both an ecotone and the latitudinal range limit for mangroves in locations where temperature is the primary governing factor (Cavanaugh et al. 2014; Osland et al. 2017b). It may also serve as a suitable boundary for monitoring the impacts of climate change, due to the capability of coastal wetland plants to rapidly respond to changes in key drivers (Lovelock et al. 2010; Wasson et al. 2013). This ecotone can be found globally on low energy, subtropical coasts where temperate salt marshes meet tropical mangroves. The salt marsh–mangrove ecotone is determined by sea level, temperature, and precipitation at regional scales, but local factors, including dispersal, are also important (Saintilan et al. 2009, 2014; Osland et al. 2017b). In the northern Gulf of Mexico, the recent expansion of mangroves into salt marshes has been linked to a decrease in the severity, duration, and frequency of freeze events, allowing for freeze-intolerant mangroves to expand poleward (Osland et al. 2013; Cavanaugh et al. 2014). Comparisons between salt marshes and invading mangrove ecosystems have been made to predict the future implications of mangrove expansion on soil, vegetation, and both aboveground and belowground carbon dynamics (Perry and Mendelssohn 2009; Comeaux et al. 2012). Other studies have examined the structural, spatial, or temporal components of this gradient on these properties and processes (Stevens et al. 2006; Osland et al. 2012; Doughty et al. 2016; Kelleway et al. 2016; Yando et al. 2016; Gabler et al. 2017; Simpson et al. 2017), and regional analyses of literature-derived data have compared ecosystem properties in mangroves and salt marshes (Feher et al. 2017). However, studies explicitly examining ecotones at the individual tree level are scant and have not explored microspatial variation in aboveground and belowground vegetation metrics, belowground carbon dynamics, and rooting patterns.

The successful expansion from single individuals to larger patches over time will eventually result in a shifting range limit and ecotone in any ecosystem, unless a disturbance event results in mortality (Gosz 1993). The areal extent of

developing mangrove patches or individuals within a salt marsh is evident aboveground, but rooting extent, belowground competition, propagule dispersal ability, and the concomitant impacts on soil properties, particularly soil carbon and organic matter, are far more cryptic. Aboveground vegetation metrics in the salt marsh–mangrove ecotone are commonly measured, and soil metrics are often used to compare edaphic conditions. Rooting metrics, however, are assessed less frequently (Comeaux et al. 2012), particularly in comparison to aboveground metrics and horizontal extent of the visible ecotone. Rooting is likely to be important due to resource competition where individual or groupings of mangroves are adjacent to other habitats (e.g. salt marsh, mud-flat, salt flat, terrestrial) (Simpson et al. 2013; Howard et al. 2015), but this has not been explicitly investigated using microspatial data across the ecotone. At the salt marsh–mangrove ecotone, marsh vegetation interacts with mangroves at all life stages both aboveground and belowground. Marsh vegetation may facilitate or inhibit net expansion of mangroves by impacting resource acquisition, stress tolerance, propagule dispersal, and seedling establishment (Clarke and Hannon 1971; Kangas and Lugo 1990; McKee et al. 2007b; Pickens and Hester 2011; Peterson and Bell 2012, 2015). Finally, soil organic matter and carbon density have been shown to have no difference between salt marsh and mangrove ecosystems in the productive tidal saline wetlands of Louisiana and Florida (Perry and Mendelssohn 2009; Henry and Twilley 2013; Doughty et al. 2016) or along a structural forest gradient in either location (Yando et al. 2016), but this has not been tested at the individual tree scale. Only by understanding these responses, feedbacks, and interactions, in both the aboveground and belowground environment, will we be better able to address how this expansion occurs at both local and landscape scales (Wiens et al. 1985).

In this study, we examine plant–soil interactions within a shifting mangrove range limit and ecotonal transition from salt marsh to mangrove at the individual tree scale. This fine-scale assessment broadly addresses whether individuals of a species expanding into incumbent habitats have the same proportional relationship and extent aboveground and belowground. We hypothesized that, at the microspatial scale, (1) belowground extent would exceed aboveground extent, (2) larger trees would have greater belowground extent, (3) differences in salt marsh species and overall structural density would differentially influence aboveground and belowground mangrove dynamics, including seedling distribution, and (4) soil properties, specifically organic matter and soil carbon density, would not differ across the salt marsh–mangrove interface within our study sites.

Methods and materials

Study area

In the summer of 2013, we established field sites at two locations in the northern Gulf of Mexico where *Avicennia germinans*, the most freeze-tolerant mangrove species in the region, reaches its latitudinal limit and forms an ecotone with salt marsh species. Field site locations included Port Fourchon, Louisiana (29.11°N, 90.20°W; adjacent to Bayou Lafourche) and Cedar Key, Florida (29.14°N, 83.03°W; between Cedar Key and Scale Key) (Online Resource 1). Both locations are microtidal with mean tidal ranges of 0.37 m (Port Fourchon, Louisiana) and 0.86 m (Cedar Key, Florida) (NOAA 2014a, b). Salt marsh vegetation in the Louisiana sites is exclusively dominated by *Spartina alterniflora*, whereas the Florida sites contain a mixture of *Batis maritima*, *Paspalum vaginatum*, *Salicornia depressa*, and *S. alterniflora* (Yando et al. 2016).

Experimental design

At each of the two locations, we identified six mangrove trees forming a discrete boundary with the surrounding salt marsh. Three replicate trees were of the large size class and three replicate trees were of the small size class, for a total of twelve trees across both locations and six trees per location. Tree sizes were relative to location. All trees were reproductive adults and represented the variation of mangrove individuals growing solitarily in salt marsh within each location. At each tree, we established a transect at the edge of the canopy (hereafter, the salt marsh–mangrove interface), positioned at 0 m and sampled 0.2-m² (0.15 m × 1.33 m) plots at set distances from each individual tree (−4, −2, −1, −0.5, 0, 0.5, 1, 2, and 4 m) (Fig. 1). The transect extended outwards into the salt marsh and inwards under the mangrove canopy. Plots in the salt marsh were assigned positive values that denote their distance from the salt marsh–mangrove interface, whereas mangrove plots were assigned negative values that denote their distance, in the opposite direction, from the salt marsh–mangrove interface. In cases where we found mangrove pneumatophores, the aerial roots of *A. germinans*, extending to the 4-m plot in the salt marsh, additional plots were added on the transect until pneumatophores could no longer be found (e.g. at 8 m and 16 m). For small individuals, if the transect extended beyond the main trunk of the tree prior to the −4, −2, or −1 m plots, those plots were eliminated. The rectangular plots were oriented with the long axis of the plot perpendicular to the transect.

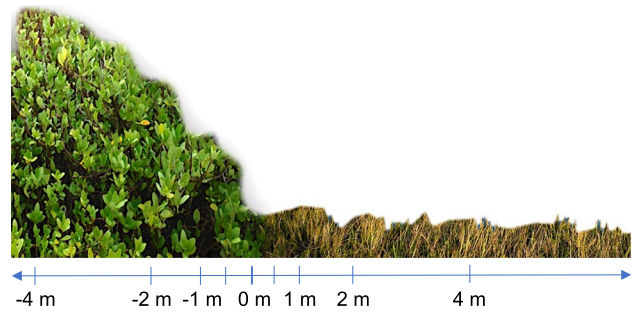


Fig. 1 Idealized transect at each mangrove extending both under the mangrove canopy and out into the surrounding salt marsh. Color version of this figure is available online

Vegetation

Aboveground, we characterized mangrove and salt marsh plant community composition and structure within each plot. For mangroves, percent cover, number of pneumatophores, number of seedlings (i.e. trees less than 1.4 m in height), and maximum canopy height were measured at each plot along the transect. For salt marsh, we measured percent vegetation cover by species. We also collected aboveground vegetation from a 0.05-m² subplot (0.15 m × 0.33 m). Upon returning to the lab, the collected vegetation was used to determine stem densities and individual heights for each species.

Belowground, we characterized mangrove and salt marsh root biomass. A 30-cm deep, 4.7-cm diameter soil core was collected from the edge of each plot for root analyses so not to disturb vegetation for possible future monitoring. Rooting in this region occurs primarily in the top 30 cm, with the majority of roots occurring in the top 15 cm of soil (Darby and Turner 2008), but we acknowledge that we may be underestimating total root biomass. Cores were collected using a custom stainless-steel piano-hinge corer and stored on ice while in the field. Upon return to the laboratory, we transferred samples to a 4 °C refrigerator until analyses were conducted. Roots were washed of soil, sorted into macro (> 2 mm) and micro (< 2 mm) size classes, and then sorted as either live or dead. Live roots were identified by color, turgor, and connectivity. Macro size class roots were identified as either salt marsh or mangrove. All analyses presented here focus on the macro size class.

Hydrology

We determined the percentage of time the soil surface was flooded (hereafter, percent time flooded) by relating elevations of each plot to local hydrological data. Elevation was determined using a laser level (Spectra Precision Laser, LL300, Trimble Navigation Ltd., Sunnyvale, CA, USA) and was then related to stable benchmarks which had previously

been determined using real-time kinematic survey (RTK; NAVD88 Geoid 12A) (Trimble R8 Receiver and Trimble TSC3 Controller, Trimble Navigation, Ltd., Sunnydale, California). For each location, local tidal gauges were utilized to determine hourly water levels for 5 years prior to September 2013 (Cedar Key, FL- NOAA [National Oceanic and Atmospheric Administration], Tides and Currents-Station ID: 8727520; Port Fourchon, LA- CRMS [Coastal Reference Monitoring System]-Station ID: CRMS0292). All water level data were collected and reported in NAVD88-Geoid 12A.

Soil and porewater properties

For soil physicochemical analyses, we collected a 15-cm deep, 4.7-cm diameter soil core from the edge of each plot. Cores were collected and stored using the same methods as previously described for the root cores. Physicochemical analyses for the soil core included quantification of soil organic matter (SOM) and soil inorganic carbon (SIC), determined via loss on ignition in a muffle furnace at 475 °C for 16 h and 800 °C for 16 h, respectively (Wang et al. 2011). Soil bulk density was determined by simple dry weight to volume ratios (Blake and Hartge 1986), after drying soils at 65 °C until a constant mass was achieved. Soil percent moisture was derived using the dry and wet weights. Soil total carbon (TC) was calculated from the SOM data using the following equation that was developed using data from these sites (data from Yando et al. 2016) ($TC = 0.02818 + 0.4053606 \cdot SOM$) (Online Resource 2). Since bulk densities differ between these two locations, TC was converted to carbon density (i.e. mg C per cm³) (C density). Soil salinity, pH, and conductivity were analyzed in the laboratory from a 1:2 soil dry weight to water ratio slurry (Jones 1999), and soil porewater temperature was measured in situ in the field using a handheld meter (YSI 30, YSI Inc., Yellow Springs, OH and Oakton WD 35801-00, Oakton Instruments, Vernon Hills, IL).

Data analyses

Regression analyses (logistic, Gaussian peak, exponential, and linear) were conducted for each location and mangrove size class. Dependent variables included mangrove and salt marsh cover, mangrove and salt marsh live root biomass, density of mangrove seedlings, density of salt marsh stems, density of mangrove pneumatophores, total structural density (i.e. the sum of salt marsh stem, mangrove seedling, and mangrove pneumatophore density), and maximum pneumatophore extent from the salt marsh–mangrove interface. Independent variables included transect plot position or maximum mangrove height. Models were selected using AICc values and weights. For models where values and

weights were similar, the simplest and most ecologically relevant model was selected for direct comparison. All non-linear regressions have R^2 values reported despite being a pseudo- R^2 , but we report them to make comparable analyses. For logistic regression, the inflection point (i.e. the peak of the first derivative) and the width of the area of greatest change (hereafter, width of AoC; the difference between the maximum and minimum peaks of the second derivative) were calculated to compare the position and width of transition zone between locations and mangrove size classes (for methods see Timoney et al. 1993; Hufkens et al. 2008). For Gaussian peak regression models, the peak height ($P(y)$), peak position ($P(x)$), and peak width (peak ± 2 standard deviations; P_w) were derived to compare locations and mangrove size classes. Standard errors of the mean are presented throughout the manuscript, included in figure error bars. Analysis of variance and Tukey's post hoc tests for other comparisons and analysis of regression models were conducted in RStudio (Team RStudio 2017) and JMP Pro 13 (SAS Institute Inc., Cary, North Carolina).

Results

Vegetation

Mean maximum canopy heights in Florida were 5.06 ± 0.59 m and 2.16 ± 0.29 m for large and small mangroves, respectively. In Louisiana, mean maximum canopy heights were 1.55 ± 0.13 m and 1.09 ± 0.10 m for large and small mangroves, respectively. At both locations and for both size classes, mangrove vegetation cover followed a decreasing logistic pattern across transects (Fig. 2). The inflection point for mangrove cover was less than 0.5 m for all locations and size classes, and the width of the AoC only increased slightly with increasing tree height (Fig. 2; Table 1).

Maximum salt marsh canopy height was almost twice as tall in Louisiana than Florida ($F_{1,11} = 113.7$, $p < 0.0001$) (Table 2, Online Resource 3). At both locations and for both size classes, salt marsh cover increased logistically across the transects (Fig. 2). Salt marsh cover in Florida large mangrove transects displayed a shifted inflection point and increased width of AoC compared to all other locations and size classes, not reaching its horizontal asymptote until 16 m from the salt marsh-mangrove interface (Fig. 2a; Table 1). All other transects had inflection points for salt marsh cover much closer to the salt marsh-mangrove interface and narrower AoC widths (Fig. 2b–d; Table 1).

Belowground live mangrove root biomass declined with increasing distance from the mangrove–marsh interface in all transects, except for Louisiana small transects (Fig. 3; Table 1). Louisiana small transects did not change in mangrove live root biomass across the transect (Fig. 3d). In

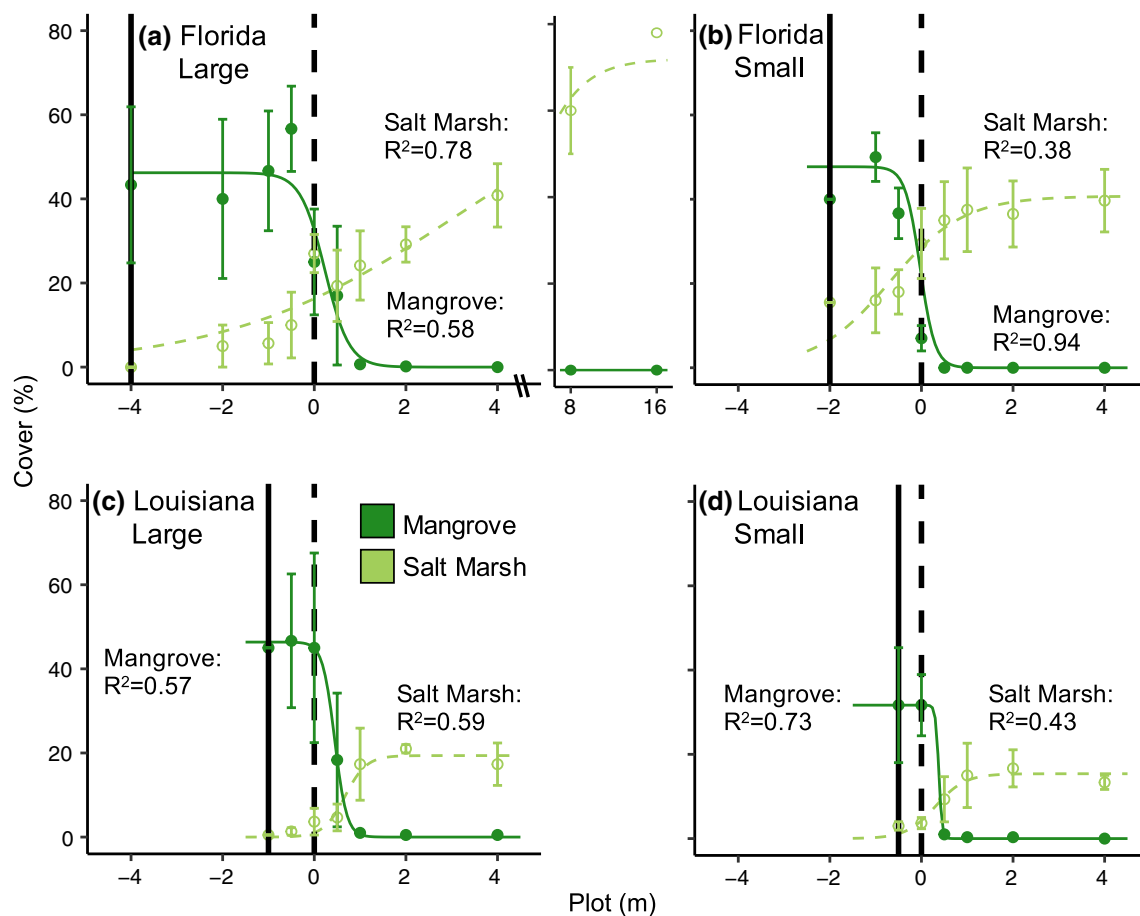


Fig. 2 Comparison of vegetative cover of mangrove (solid line-dark green filled symbols) and salt marsh (dashed line-light green open symbols) plots across the salt marsh-mangrove interface in **a, b** Florida and **c, d** Louisiana using a logistic regression. Values are mean \pm SE ($N = 3$). Transects were established at the edge of the canopy,

positioned at 0 m (vertical dashed line) and sampled plots at set distances from either **b, d** small or **a, c** large trees. Note that panel **a** extends to 16 m and has a break between the 4 and 8 m plots. Color version of this figure is available online

Florida, live mangrove roots extended out to the 8- and 4-m plots in large and small mangroves, respectively (Fig. 3a, b). Additionally, mangrove pneumatophores aboveground were found as far as the 8-m plot in Florida large mangrove transects and 2-m plot in Florida small mangrove transects, but were absent after the 1-m plot in Louisiana large mangrove transects and the 0.5-m plot in Louisiana small mangrove transects. There was a positive logistic relationship between maximum mangrove height and maximum mangrove pneumatophore extent (Fig. 4). Salt marsh live roots extended across the salt marsh-mangrove interface under the mangrove canopy in all cases (Fig. 3a, b, d) except for large Louisiana mangroves (Fig. 3c). Large Louisiana mangrove transects had very limited salt marsh roots present, even in areas exclusively dominated by salt marsh (Fig. 3c).

Mangrove seedling density in Florida followed a Gaussian peak distribution in both large and small mangrove transects (Fig. 5a, b). Both Florida transects had their

position of maximum density ($P(x)$) centered within the mangrove side of the interface, at approximately the -1 m plot, with the maximum density four times greater ($P(y)$) and the peak width (distribution width; P_w) twice as wide in large mangrove transects than small mangrove transects (Fig. 5a, b; Table 1). Structural density in Florida did not have any trend, but remained consistently high at approximately 300 units per m^2 (Fig. 5a, b; Table 1) regardless of size. Louisiana large mangrove transects had a linear increase in mangrove seedling density beyond the salt marsh-mangrove interface, while Louisiana small mangrove transects displayed no pattern in seedling density distribution (Fig. 5c, d; Table 1). Structural density in both Louisiana mangrove transect types followed an exponential decrease across the salt marsh-mangrove interface (Fig. 5c, d; Table 1), with structural density higher beneath larger mangroves. Salt marsh reaches of the Louisiana transects had almost an order of magnitude lower

Table 1 Summary of model parameters used to describe changing abundances of large and small mangroves in Florida and Louisiana

Metric type	Location	Size class	Model type	R^2	F -statistic	Inflection point (m)	Width of AoC (m)	Peak location (m)	Peak width (m)
Mangrove cover (%)	Florida	Large	Logistic	0.58		0.23	0.70		
		Small	Logistic	0.94		− 0.03	0.43		
	Louisiana	Large	Logistic	0.57		0.45	0.35		
		Small	Logistic	0.73		0.38	0.09		
Salt marsh cover (%)	Florida	Large	Logistic	0.78		3.11	6.66		
		Small	Logistic	0.37		− 0.69	2.13		
	Louisiana	Large	Logistic	0.59		0.67	0.62		
		Small	Logistic	0.4		0.31	0.85		
Mangrove live root biomass (g)	Florida	Large	Linear	0.14	5.9*				
		Small	Linear	0.12	3.8 [‡]				
	Louisiana	Large	Linear	0.24					
		Small	Linear	0.16					
Salt marsh live root biomass (g)	Florida	Large	Linear	0.06	3.1 [‡]				
		Small	Linear	0.33	11.3**				
	Louisiana	Large	No pattern	NS					
		Small	No pattern	NS					
Structural density (N m ^{−2})	Florida	Large	No pattern	NS					
		Small	No pattern	NS					
	Louisiana	Large	Exponential	0.67	37.39**				
		Small	Exponential	0.53	19.99**				
Seedling density (N m ^{−2})	Florida	Large	Gaussian	0.33				− 1	4
		Small	Gaussian	0.8				− 1.25	1.75
	Louisiana	Large	Linear	0.3	7.3*				
		Small	No pattern	NS					
Salt marsh density (N m ^{−2})	Florida	Large	Logistic	0.73		− 0.27	1.64		
		Small	Logistic	0.49		− 0.8	0.6		
	Louisiana	Large	Linear	0.2	4.1 [‡]				
		Small	Linear	0.28	6.2*				
Pneumatophore density (N m ^{−2})	Florida	Large	Exponential	0.8	121.1**				
		Small	Exponential	0.83	101.4**				
	Louisiana	Large	Exponential	0.84	93.2**				
		Small	Exponential	0.68	37.6**				

p -values are represented for linear and exponential regressions only ($\ddagger p < 0.09$; $*p < 0.05$; $**p < 0.01$)

structural density (i.e., ~ 25–50 units per m²) compared to their Florida counterparts (Fig. 5). In both locations and size classes, pneumatophore density declined exponentially along the transect (Table 1; Online Resources 4–7). In Florida, salt marsh stem density followed an increasing logistic distribution for both large and small mangrove transects with an asymptote at approximately 500 stems per m² (Table 1; Online Resources 4, 5). In Louisiana, salt marsh stem density decreased in large mangrove transects and small mangrove transects (Table 1; Online Resources 6–7).

Hydrology, soil properties, and porewater

Hydrology, elevation, and soil properties did not differ along the transect from mangrove to salt marsh in any location or size class; differences were most often only between locations (Online Resource 3). Louisiana elevations were ~ 35 cm lower in elevation, and percent time flooded in Louisiana was three times greater compared to Florida (Table 2; Online Resource 3). Florida had ~ 10% greater soil moisture and twice as much SOM than Louisiana (Table 2; Online Resource 3). Carbon density in Florida was a third greater than in Louisiana (Table 2; Online Resource 3).

Table 2 Comparison of variables used to evaluate environmental differences for Large and Small trees in Florida and Louisiana

	Florida		Louisiana	
	Large	Small	Large	Small
Vegetation				
Max. salt marsh height (m)	0.46 ± 0.03^b	0.48 ± 0.01^b	1.18 ± 0.07^a	1.04 ± 0.09^a
Hydrology (2008–2013)				
Elevation (m)	0.42 ± 0.01^a	0.41 ± 0.01^a	0.05 ± 0.003^b	0.05 ± 0.004^b
Time flooded (%)	14.8 ± 0.7^b	15 ± 0.5^b	46.5 ± 0.7^a	45.5 ± 0.7^a
Soil properties				
Bulk density (g cm^{-3})	0.3 ± 0.005^b	0.3 ± 0.005^b	0.4 ± 0.01^a	0.5 ± 0.01^a
Soil moisture	77.5 ± 0.3^a	77 ± 0.2^a	66.7 ± 0.7^b	64.8 ± 0.9^b
SOM (%)	29.7 ± 0.4^a	28.1 ± 0.4^a	13.1 ± 0.5^a	11.8 ± 0.3^a
C density (mg cm^{-3})	30 ± 0.3^a	30 ± 0.5^a	20 ± 0.7^b	20 ± 0.4^b

Values are means (\pm SE, $N = 3$). Significant differences ($p < 0.05$) are denoted by different lower case letters within each metric across all tree sizes and locations

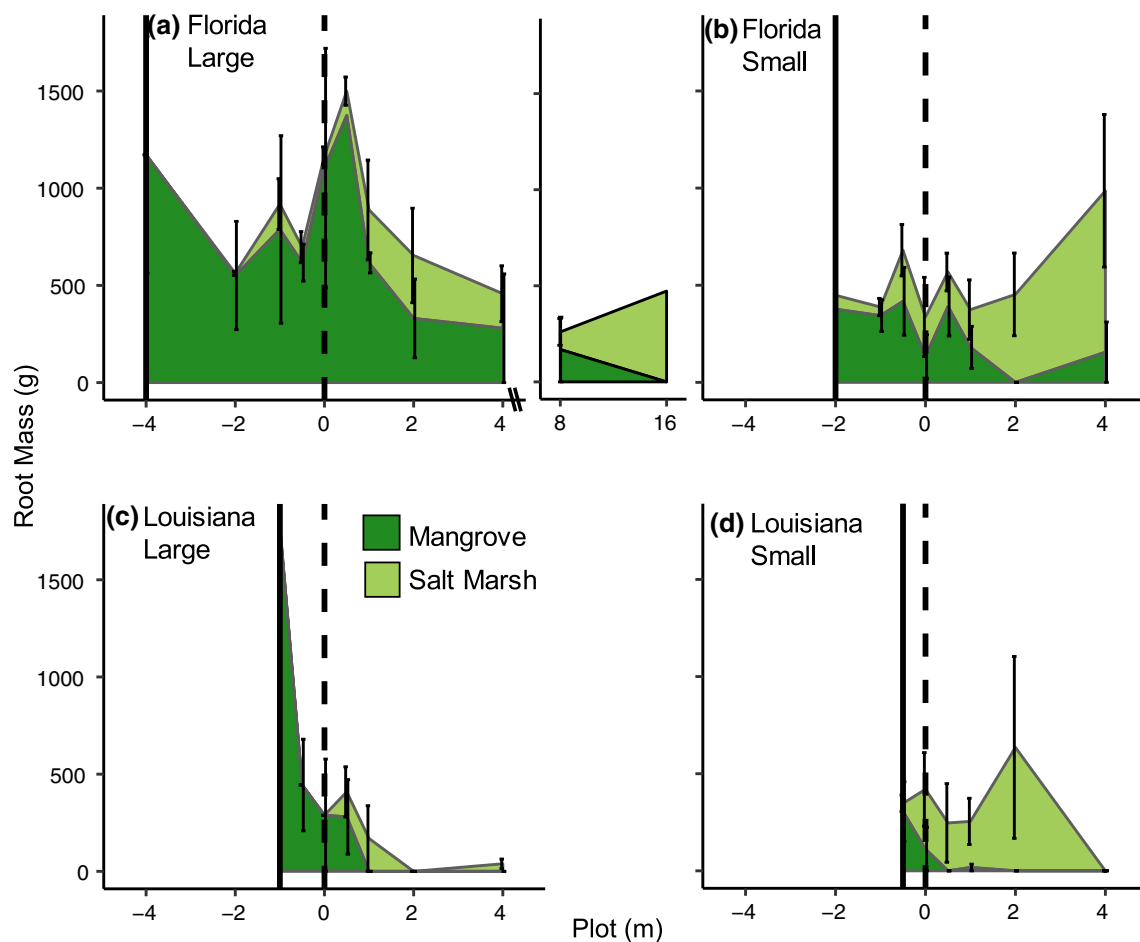


Fig. 3 Comparison of live root biomass (stacked) of mangrove (dark green) and salt marsh (light green) plots across the salt marsh-mangrove interface in **a, b** Florida and **c, d** Louisiana. Values are mean \pm SE ($N = 3$). Transects were established at the edge of the canopy

and positioned at 0 m (vertical dashed line) and sampled plots at set distances from either **b, d** small or **a, c** large trees. Note that panel **a** extends to 16 m and has a break between the 4 and 8 m plots. Color version of this figure is available online

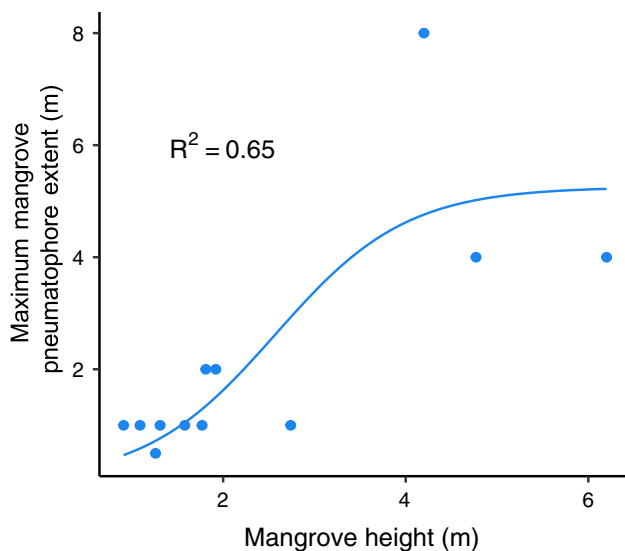


Fig. 4 Maximum mangrove canopy height by maximum mangrove pneumatophore extent. All locations and size classes combined and each point represents an individual transect. Inflection point = Mangrove height of 2.6 m, Width of Area of Change = 1.8 m. Color version of this figure is available online

Louisiana had slightly greater overall bulk density compared to Florida (Table 2; Online Resource 3). Other soil and pore-water variables also differed by location (Online Resource 8), but never by transect position (Online Resources 3,8).

Discussion

The results of our study highlight key differences between aboveground and belowground vegetation pattern and extent, the importance of salt marsh type and total structural density, and site-specific homogeneity in key soil metrics across the salt marsh–mangrove interface. The location-specific nature of many of our findings shows the complexity of this range limit and ecotone even within the same region.

Aboveground mangrove and salt marsh vegetation cover followed logistic patterns of change along the transect, similar to the sigmoidal wave hypothesis/relationship reported in other ecotones (Cairns and Waldron 2003; Danz et al. 2013). Differences between the logistic regression in mangrove cover can be attributed to tree size, with the largest overall trees, those of the Florida large mangrove transects, also suppressing salt marsh species and resulting in a shifted pattern due presumably to competition for light (Lett and Knapp 2003) and other resources (Belsky 1994). The comparatively smaller stature of mangroves in the Florida small, Louisiana large, and Louisiana small transects resulted in smaller aboveground areal extents and did not influence salt marsh vegetation as much as their Florida large mangrove

counterparts, likely due to limited light and less belowground competition (Fig. 1b–d) (Pickens 2012).

Neither mangrove nor salt marsh live belowground root biomass followed the logistic pattern seen in aboveground cover metrics. Mangrove live root biomass declined in all transects, but differed in horizontal extent. The disparities in mangrove and salt marsh live root biomass, and tree sizes, are likely due to a combination of duration of time since the establishment of these mangroves, local mangrove growth rates, and species-specific salt marsh interactions (Lovelock et al. 2007, 2010; Bulmer et al. 2016), similar to that of other forest systems (Hodgkins and Nichols 1977). Older mangroves and/or those with greater growth rates are likely to have had a greater opportunity for horizontal expansion and increased live root biomass within a local area, where soil and edaphic conditions are similar. Although we do not have accurate age estimates of these mangroves, due to the difficulty in aging individual mangroves of all species (Tomlinson 1994), our Florida location had much taller mangroves than our Louisiana location (Yando et al. 2016). We acknowledge that size class does not necessarily translate to age, but in this case, larger trees had a greater maximum pneumatophore extent (Fig. 4). The relationship between mangrove height and pneumatophore extent follows a logistic pattern. The pattern represented is a conservative estimate of this relationship as the asymptote may continue to rise or may shift with the inclusion of more data, particularly of larger trees (i.e. trees greater than 6 m in height). In addition to mangrove height, salt marsh species, density, and their ability to compete for space and resources belowground may also impact the ability for mangroves to expand belowground (Howard et al. 2015). During early life stages, Louisiana's *S. alterniflora*-dominated salt marshes have been shown to potentially compete with *A. germinans* belowground through their high specific root area and ability to inhibit the development of complex mangrove root architecture (McKee and Rooth 2008; Pickens 2012). The Florida salt marshes, dominated by a variety of grasses and succulents, had mangrove roots extending well into the salt marsh. The lack of salt marsh roots in large mangrove transects in both sites can likely also be attributed to age and development. Age, growth rate, and salt marsh interactions taken together start to provide an explanation for live root biomass patterns, but certainly deserve greater attention, particularly at the individual mangrove level. Research on individual shrubs in grassland systems and trees in savanna systems have highlighted the importance of belowground interactions for understanding aboveground patterns (Van der Putten 2012).

In addition to potential belowground interactions, aboveground seedling distribution of mangroves in our study appears to be controlled by surrounding vegetation structural density and percentage of time flooded. In Florida,

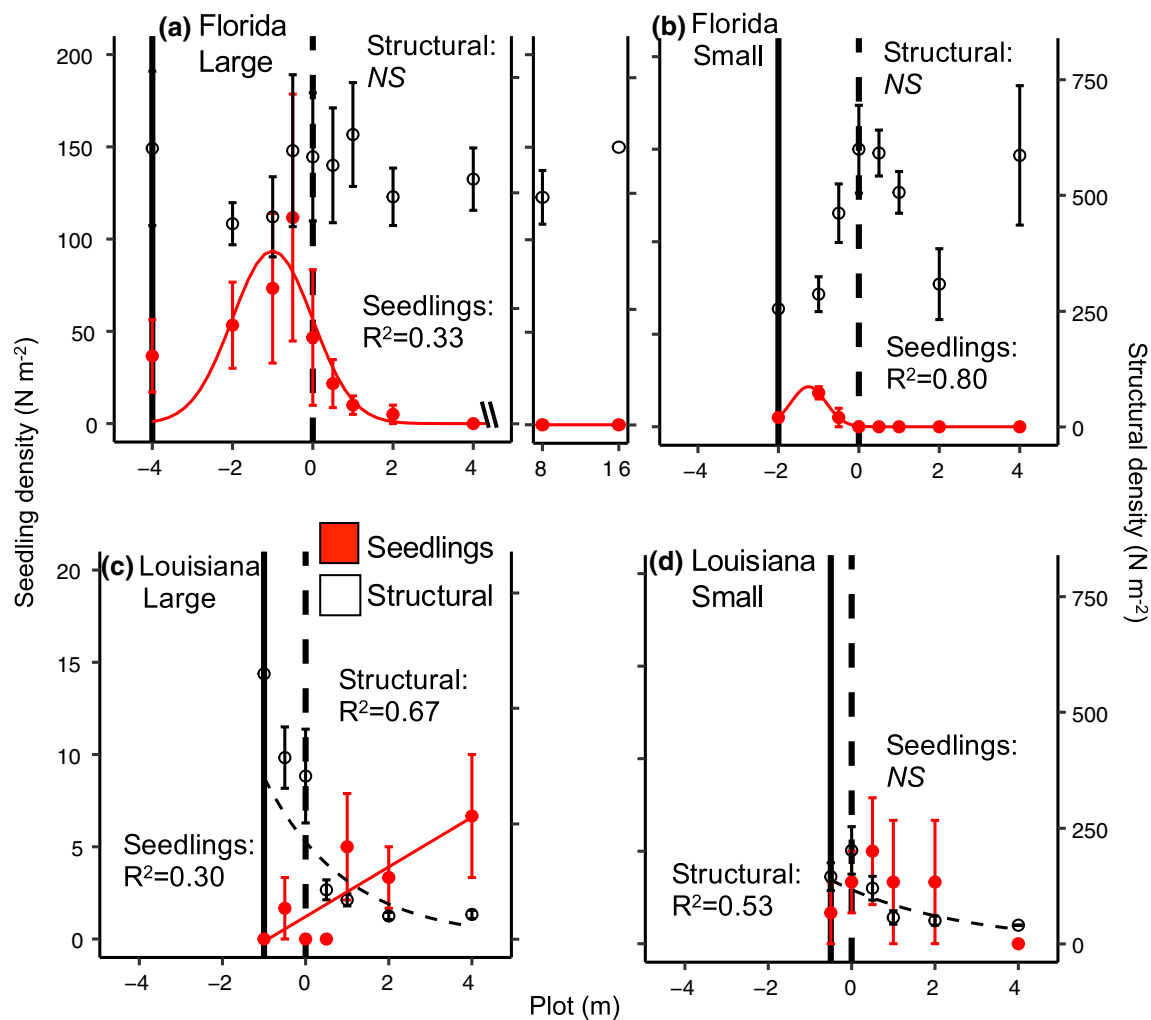


Fig. 5 Comparisons of mangrove seedling (solid line-red symbols; left y axis) and total structural (dashed line-open white symbols; right y axis) density across the salt marsh-mangrove interface in **a, b** Florida and **c, d** Louisiana. Values are mean \pm SE ($N = 3$). Transects were established at the edge of the canopy and positioned at 0 m (ver-

tical dashed line) and sampled plots at set distances from either **b, d** small or **a, c** large trees. Note that panel **a** extends to 16 m and has a break between the 4 and 8 m plots. Color version of this figure is available online

high structural density across the entire transect and minimal inundation limit the ability for propagules to disperse away from the parent tree. The absence of seedlings in the interior mangrove areas is likely due to light limitation under the mature mangrove canopy (Smith 1987; Clarke and Allaway 1993), thus resulting in a peak density of seedlings just before the transition from mangrove to salt marsh as propagules are unable to disperse with high overall structural density. Conversely, our Louisiana site's rapidly declining structural density and greater percentage of time flooded allow for greater dispersal and establishment of mangrove propagules away from the parent mangrove. The increased density of seedlings in large Florida mangroves is likely due to the greater number of propagules produced on such large trees (Alleman and Hester 2011a) and the possibility of cold temperature protection offered by these large canopies to

seedlings found underneath (Krauss et al. 2008; Ross et al. 2009; D'Odorico et al. 2013; Devaney et al. 2017). This protection of seedlings to disturbance by larger trees has previously been described as a 'shield effect' in both freeze events (Ross et al. 2009) and hurricanes (Imbert et al. 1996). The pattern of high seedling densities at the salt marsh-mangrove interface in Florida is similar to the findings by Stevens et al. (2006) who completed their study in nearby islands off Cedar Key, Florida. The difference in structural density can largely be attributed to salt marsh vegetation type. In the salt marsh, Florida's high structural density was composed of a mixture of *B. maritima*, *P. vaginatum*, *S. depressa*, and *S. alterniflora*, while Louisiana's low structural density was solely dominated by *S. alterniflora* (Yando et al. 2016). Underneath the mangrove canopy, large numbers of pneumatophores contribute to the high structural

densities, except for Louisiana's small mangrove individuals, which had few pneumatophores. The combination of flooding and vegetation structure has also been suggested to be important for trapping mangrove propagules upslope as mangroves migrate inland with sea level rise (Peterson and Bell 2012, 2015), within disturbed mangrove settings (McKee et al. 2007a), and recently restored sites (Donnelly and Walters 2014). Others have also suggested that high structural density not only limits dispersal, but may also limit establishment of propagules as they are not able to root prior to desiccation (Howard et al. 2015). Comparably, within mangrove forests containing species with prop roots, density of prop roots plays an important structural role in trapping propagules and limiting dispersal (Van der Stocken et al. 2015). Vegetation density may have both positive and negative implications for mangrove dispersal, establishment, and growth depending on seasonality, location, and life history stage in mangroves (Stevens et al. 2006; Alleman and Hester 2011b; Pickens 2012) and other plant communities (Holmgren et al. 1997; Van Auken 2000). The impact of combined abiotic and biotic interactions is needed to understand dispersal once temperature limitations are released in this system and differences in the transition may be observable (similar to Walker et al. 2003), but require an objective measurement and comparison within and between locations.

Finally, soil metrics, specifically SOM and C density, did not change across the salt marsh–mangrove interface or with mangrove size class, but rather only between locations. These findings corroborate previous studies that suggest that SOM and C density do not differ in these locations between salt marsh and mangroves (Perry and Mendelsohn 2009; Henry and Twilley 2013; Doughty et al. 2016) or with mangrove structural development (Yando et al. 2016) in areas with mesic, productive salt marshes. We might expect to see changes in SOM and C density across the interface with mangroves in drier or upslope locations dominated by less productive salt marsh species (Comeaux et al. 2012; Kelleway et al. 2016; Yando et al. 2016). These findings also fit well into the broader discussion of the impacts on soil carbon of woody encroachment into grasslands with mesic locations often seeing no net change (Briggs et al. 2005) or even a decrease (Jackson and Caldwell 1993), while increases are observed in semi-arid and arid locations (Eldridge et al. 2011). Future shifts in the salt marsh–mangrove ecotone are unlikely to result in changes to these key soil properties in these mesic locations.

The findings of our study highlight the importance of examining ecotones at small microspatial scales, connecting them to broader ecosystem patterns, both in vegetation and soil properties, and realizing site specific differences. By studying “boundary dynamics”, as stated by Wiens et al. (1985), we can advance understanding of local

dynamics that affect landscape level processes. Within the mangrove range limit and salt marsh–mangrove ecotone, the disconnect in pattern between aboveground vegetation cover and belowground rooting metrics illustrates that aboveground vegetation is not sufficient to characterize shifts in ecosystems. Additionally, variation in the interactions with the incumbent surrounding vegetation, in this case the salt marsh ecosystem, can differentially influence expansion rates via dispersal, establishment, and competition even within the same region, thus providing a greater understanding to the drivers that influence mangrove expansion beyond just temperature and precipitation (Giri and Long 2016; Osland et al. 2017a). Surrounding vegetation and hydrology appear to be controlling the distribution of mangrove dispersal, but further research is needed to better understand short distance dispersal, individual tree expansion rates, and the impact of microclimates formed during non-lethal freeze events. The interaction between salt marshes and mangroves is far more complex than simple invasion, shading, and competition regardless of the scale being examined. Finally, the key soil metrics of SOM and C density are not likely to change with mangrove expansion into mesic, productive salt marshes. By understanding changes, or a lack thereof, at an individual level across an ecotone, we are better able to predict ecotonal dynamics and the implications of a range shift at broader scales, as well as connect aboveground and belowground patterns as invading vegetation expands into incumbent ecosystems with global change.

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Compliance with ethical standards

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