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Title: Will Fluctuations in Salt Marsh - Mangrove Dominance Alter Vulnerability of a Subtropical Wetland to Sea-Level Rise?

Running Title: Vegetation Shifts and Sea-Level Rise

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Type of Paper: Primary Research Article

Abstract

To avoid submergence during sea-level rise, coastal wetlands build soil surfaces vertically through accumulation of inorganic sediment and organic matter. At climatic boundaries where mangroves are expanding and replacing salt marsh, wetland capacity to respond to sea-level rise may change. To compare how well mangroves and salt marshes accommodate sea-level rise, we conducted a manipulative field experiment in a subtropical plant community in the subsiding Mississippi River Delta. Experimental plots were established in spatially equivalent positions along creek banks in monospecific stands of *Spartina alterniflora* (smooth cordgrass) or *Avicennia germinans* (black mangrove) and in mixed stands containing both species. To examine the effect of disturbance on elevation dynamics, vegetation in half of the plots was subjected to freezing (mangrove) or wrack burial (salt marsh), which caused shoot mortality. Vertical soil development was monitored for six years with the surface elevation table-marker horizon system. Comparison of land movement with relative sea-level rise showed that this plant community was experiencing an elevation deficit (i.e., sea level was rising faster than the wetland was building vertically) and was relying on elevation capital (i.e., relative position in the tidal frame) to survive. Although *Avicennia* plots had more elevation capital, suggesting longer survival, than *Spartina* or mixed plots, vegetation type had no effect on rates of accretion, vertical movement in root and sub-root zones, or net elevation change. Thus, these salt marsh and mangrove assemblages were accreting sediment and building vertically at equivalent rates. Small-scale disturbance of the plant canopy also had no effect on elevation trajectories— contrary to work in

peat-forming wetlands showing elevation responses to changes in plant productivity. The findings indicate that in this deltaic setting with strong physical influences controlling elevation (sediment accretion, subsidence), mangrove replacement of salt marsh, with or without disturbance, will not necessarily alter vulnerability to sea-level rise.

Introduction

One of the consequences of global warming is an increase in sea level, which affects coastal wetlands worldwide (IPCC, 2014). To avoid submergence, low-lying ecosystems must maintain their soil surfaces in relation to changes in relative sea level, which involves the combined movements of ocean and land surfaces. Rates of sea-level rise (SLR) have increased globally from 1.1 mm yr^{-1} (1902 to 1990) to 3.1 mm yr^{-1} (1993 to 2012) (Dangendorf *et al.*, 2017). Regional trends in ocean height are not equal, however, due to geographic variation in glacial isostatic adjustment and non-uniform changes in ocean thermal expansion (Cazenave & Llovel, 2010). In addition, local land movements, caused by processes such as shallow subsidence or fluid withdrawal, can lead to more rapid submergence of the land surface in some geographic locations. For example, high rates of subsidence (9 mm yr^{-1}) in the Mississippi River Delta (MRD) (Nienhuis *et al.*, 2017), combined with a change in ocean height, yield submergence rates greater than 1 cm yr^{-1}. To counterbalance the combined effects of SLR and local land movement (i.e., relative SLR), soil surfaces in coastal wetlands must build vertically at an equivalent rate.

Many coastlines are fringed by wetlands such as salt marshes or mangroves, and their distributions overlap at subtropical latitudes. In both mangrove and salt marsh habitats, physical processes of mineral sedimentation and biological processes of organic matter accumulation (peat formation) aid in counterbalancing relative SLR (e.g., Neubauer, 2008; McKee, 2011). When SLR rates exceed rates of vertical land development, however, excessive flooding leads to mortality of the emergent vegetation (Mendelssohn & McKee, 1988; Mendelssohn & Morris,

2000) and to eventual wetland loss (Turner & Rao, 1990; Delaune *et al.*, 1994; Couvillion *et al.*, 2017). Demise of the plant community contributes to a further lowering of the soil surface, due to lack of organic inputs and/or to decreased sediment trapping (Cahoon *et al.*, 2003; Krauss *et al.*, 2003; Baustian *et al.*, 2012). An understanding of how different types of wetland vegetation may respond to SLR is essential to accurate predictions of future submergence of coastal regions. Such information is particularly important for major vegetation boundaries where changes in the plant community may be occurring in response to climate change.

Mangroves, particularly the genus *Avicennia*, have extended their range and replaced salt marsh in several locations, including the USA, Peru, Australasia, Africa, China, and South Africa (reviewed by Saintilan *et al.*, 2014). Mangrove expansion may be mediated by propagule dispersal patterns (Patterson *et al.*, 1997; Peterson & Bell, 2015), biotic interactions (facilitation, competition, predation) (Patterson *et al.*, 1997; McKee & Rooth, 2008; Guo *et al.*, 2013; Simpson *et al.*, 2013; Langston *et al.*, 2017), climate extremes (freezes, droughts) (Patterson & Mendelssohn, 1991; Patterson *et al.*, 1993; McKee *et al.*, 2004; Cavanaugh *et al.*, 2014), rising sea level (Krauss *et al.*, 2011), and human modifications of hydrology (Krauss *et al.*, 2011). At salt marsh-mangrove boundaries along the northern Gulf of Mexico, species shifts are driven primarily by weather extremes and periodic disturbances by storms (Stevens *et al.*, 2006). Mangroves are sensitive to cold temperatures and are killed by freezing (McMillan & Sherrod, 1986; Stevens *et al.*, 2006; Ross *et al.*, 2009). One of the most cold-tolerant mangrove species is *Avicennia germinans* (L.) L. (Markley *et al.*, 1982; McMillan & Sherrod, 1986). Although freezing damages the canopy, *A. germinans* recovers during intervening warm periods (Stevens *et al.*, 2006). Mangrove range expansion (Comeaux *et al.*, 2012; Saintilan *et al.*, 2014; Armitage *et al.*, 2015) may reflect less frequent or less severe winter freezes (Meehl *et al.*, 2004; Giri *et al.*, 2011; Osland *et al.*, 2013; Cavanaugh *et al.*, 2014; Osland *et al.*, 2017). Salt marsh perennials (grasses, sedges, rushes) can tolerate periodic freezing, but may die due to other factors. A common, small-scale disturbance to salt marsh vegetation is burial by wrack (plant debris), which

smothers the vegetation (Valiela & Rietsma, 1995; Pennings & Richards, 1998; Minchinton, 2002). Because the dominant salt marsh species, *Spartina alterniflora* Loisel., is a strong competitor of *A. germinans* (Patterson *et al.*, 1993; McKee & Rooth, 2008), wrack disturbance may facilitate the expansion of mangroves by creating bare areas in the marsh. Thus, the differential effects of temperature or disturbance on co-occurring species can cause a cyclic fluctuation in relative abundance of salt marsh and mangrove vegetation (Stevens *et al.*, 2006), which may, in turn, alter vulnerability of the wetland to SLR.

Comparative information is needed about how vegetation shifts affect capacity to keep pace with relative SLR, especially if accompanied by disturbance. Such knowledge is critical for managing ecosystems at climatic boundaries and for planning restoration of deteriorating coastal wetlands at such boundaries (e.g., the subtropical wetlands of the MRD (CPRA, 2017)). Some investigators have proposed that mangrove replacement of salt marsh will improve sediment trapping and/or organic contributions to soil volume, thereby enhancing resistance to relative SLR (Rogers *et al.*, 2006; Comeaux *et al.*, 2012; Bianchi *et al.*, 2013; Saintilan *et al.*, 2014). Other work, however, has found no differences between salt marsh and mangrove stands in sediment accretion (Perry & Mendelssohn, 2009) or organic matter accumulation (Yando *et al.*, 2016). Also, although information exists about relative rates of sediment accretion and vertical land building in different wetland habitats, the data are not always comparable due to differences in geomorphic setting, climate, subsidence rate, disturbance type and frequency, human activity, and many other confounding factors that contribute to overall variation and prevent an unequivocal comparison of vegetation effects (see review by McKee *et al.*, 2012).

To begin assessing the role of vegetation type in determining the capacity of subtropical, coastal wetlands to keep pace with relative SLR, we experimentally tested whether vegetation type, with or without disturbance, can influence elevation trajectories in a salt marsh-mangrove community. A six-year study was carried out in the MRD where the black mangrove, *A. germinans*, reaches its northernmost limit in North America and intergrades with the salt marsh

grass, *S. alterniflora*. Our field experiment directly compared rates of vertical accretion (VA),

subsurface movements in root and sub-root zones, and surface elevation change (SEC) in salt

marsh areas dominated by *S. alterniflora*, mangrove stands dominated by *A. germinans*, and

mixed stands containing both species—all situated equidistant from a tidal creek within the same

hydrologic setting. In addition, small-scale disturbance was simulated by applying treatments of

freezing (mangrove) or wrack burial (salt marsh) to assess how temporary reduction in vegetative

cover might alter processes affecting elevation dynamics. The results represent an important step

toward understanding how mangrove expansion may affect habitat stability of subtropical, coastal

wetlands.

Materials and methods

Study site

The study area was located northwest of Port Fourchon, Louisiana, USA (29°08'21''N, 90

°14'19''W) (Fig. 1a) in the Barataria Basin hydrologic unit, which was formed 2,500 to 800 years

before present as part of the Lafourche delta complex (Roberts, 1997). The MRD is undergoing

high rates of subsidence (Nienhuis *et al.*, 2017) which, along with human activities (Coleman *et

al.*, 1998), has contributed to a coast-wide decrease in land area of 4,833 km^2 between 1932 and

2016 (Couvillion *et al.*, 2017). Despite high rates of land loss, saline wetlands in coastal

Louisiana are extensive, covering 2,954 km^2 (Sasser *et al.*, 2014). Salt marshes in the region are

dominated by *S. alterniflora*, but large stands of *A. germinans* exist, particularly in the Port

Fourchon area. Total mangrove area in this region of the coast has expanded substantially from

41 ha in 1993 to 670 ha in 2011 (Osland *et al.*, 2017).

Historical records indicate that *A. germinans* has been present in the region for at least

200 years. A specimen of *Avicennia americana* (syn. *A. germinans*) was collected in 1812 in

Louisiana by Thomas Nuttall and deposited in the Philadelphia Academy of Natural Sciences

Herbarium (http://plants.jstor.org/stable/10.5555/al.ap.specimen.ph00005841). One hundred years later, specimens of *A. germinans* were collected on Last Island, Louisiana on June 8, 1913 by E.C. Wurzlow and deposited in the Louisiana State University Herbarium (http://www.herbarium.lsu.edu/). One of the first descriptions of black mangroves in Louisiana was penned by Lloyd and Tracey (1901) who described mangrove stands growing "abundantly" on offshore islands, especially Breton Island. Their description suggests that these early stands were fairly short in stature—no taller than 0.6 m. Historical videos also depict black mangroves in Louisiana in 1915 (e.g., U.S. President Theodore Roosevelt was filmed walking in a black mangrove stand at Breton National Wildlife Refuge; "TR in Louisiana" (1915), Library of Congress: http://www.loc.gov/item/mp76000363). This video shows scattered trees as well as contiguous stands composed of 1.0 to 1.5 m tall mangroves growing within a few meters of open water—similar to the physiognomy and spatial position of current mangrove populations (Fig. 1b, Fig. 2a-b).

Although the mangroves in the study area were small in stature, averaging 1.5 m tall with extensive branching and stump sprouting (Fig. 2b), they were mature (i.e., reproductive) and typical of mangroves in the region. By comparison, *S. alterniflora* canopy height averaged 0.6 to 0.8 m. Buoyant propagules of *A. germinans*, carried by tides, are dispersed in late fall (November-December) and deposited on the soil surface where they can take root within days (Rabinowitz, 1978). Mangroves typically establish along creek banks (Fig. 1b, Fig. 2a) where soil elevations are highest and the opportunity for propagule stranding and survival is greatest (Patterson *et al.*, 1993; Patterson *et al.*, 1997). Wrack deposition in salt marshes also tends to occur along creek banks in coastal Louisiana (Fig. S1). Fallen, dead shoots of *S. alterniflora* are deposited by tides in linear rafts, typically at mean high water; existing mangrove stands also trap wrack (Fig. 2c, Fig. S1f). Wrack deposition varies spatially and temporally (Fig. S1), but kills *S. alterniflora* and creates unvegetated patches in the salt marsh (Fig. 2d). Mangrove propagules strand in these bare areas and gain a foothold (Fig. 2e). Patches composed of one or more

individual mangroves develop within the salt marsh matrix and, over time, enlarge and coalesce to form contiguous stands along shorelines (typical dimensions: 10-15 m wide x 100-250 m long) (Fig. 1b, Fig. 2a).

Severe winter freezes periodically cause widespread damage to mangrove populations at their northern limits (Fig. 2f, Fig. S2) (Stevens *et al.*, 2006). Greater resistance of *A. germinans* to freezing temperatures is attributed partly to a capacity to re-sprout from basal meristems (i.e., coppice) (Tomlinson, 1994), which allows rapid recovery after a freezing event (Fig. S2e). Freeze damage, however, can vary from defoliation to mortality of the entire tree if basal meristems die (Stevens *et al.*, 2006). Dieback of mangroves in Louisiana due to killing freezes has been reported since the early 1900s. For example, Lloyd and Tracy (1901) describe "large numbers" of dead mangroves in Louisiana in 1900, just after the Great Arctic Outbreak of 1899 when a low temperature of -14 °C was recorded on February 13 in New Orleans (Kocin *et al.*, 1988). Climate records show that more recent freezes occurred in south Louisiana in 1983-84 and 1989, followed by two decades without a killing freeze; in 2010 a moderate freeze occurred (New Orleans International Airport Station ID 166660, Louisiana State Office of Climatology, www.losc.lsu.edu). Extensive mortality of mangroves occurred in association with the 1983-84 freeze event (Giri *et al.*, 2011) and again in 1989 when mangrove stands in the Port Fourchon area, which had survived earlier events, were killed (KLM, personal observation). The mangrove stands in the study area (Fig. 1b) were present in the same locations and approximate configurations prior to the killing freeze of 1989 (historical aerial imagery: 1957 (U.S. Navy), November 1989 (U.S. Geological Survey, http://earthexplorer.usgs.gov) and had reestablished by 2000 (color infrared imagery, Leeville quadrangle, https://www.lacoast.gov/new/Pubs/Map_data/bm2000/index.htm). The current population in the Port Fourchon area likely reestablished from propagules that survived the 1989 freeze. Floating or stranded propagules of *A. germinans* apparently can survive low temperatures for short periods (-6.5 to 2.5 °C for 2 to 24 h; Pickens & Hester, 2011).

Surface soils (15 cm depth) in the study area had an average dry bulk density of 0.39 g cm^{-3} and 15% organic matter content; the inorganic component was composed of 66% silt, 15% sand, and 7% clay. Tides in this region are diurnal with a 0.32 m amplitude (1983-2001 Epoch; NOAA Tides and Currents Station #8761724, www.tidesandcurrents.noaa.gov). Monthly minimum temperatures varied during the study (March 2006 to March 2012) from -6 °C (January 2010) to 23.3 °C (July 2010) (New Orleans International Airport Station ID 166660, Louisiana Office of State Climatology; www.losc.lsu.edu). In January 2010, temperatures remained at or below -1.7 °C for five consecutive days. Although some mangrove stands suffered shoot mortality during this event (Fig. S2), damage was patchy along the Louisiana coast, and the mangroves in the experimental plots showed little or no visible damage. The area is occasionally affected by tropical storms and hurricanes, with Hurricanes Katrina and Rita (2005) occurring just before this study and Hurricane Gustav (2008) during the study (but caused no discernable damage to experimental plots).

Experimental design

The study was conducted along a natural creek where monospecific stretches of *S. alterniflora* were interspersed with monospecific stands of *A. germinans* as well as mixed stands where mangroves were invading salt marsh (hereafter, *Spartina*, *Avicennia*, and Mixture, respectively). Potential plot locations were identified along a 2 km stretch of the creek (Fig. 1b) and from this pool, eighteen plots were selected in May 2006. A randomized block design was used in which each of three replicate blocks (blocked on spatial position along the creek) contained all species assemblages and treatments (i.e., three vegetation types (*Spartina*, *Avicennia*, Mixture) x two disturbance treatments (control, disturbed) x three replicates). Plots (each 3 m x 5 m) were positioned on the creek bank equidistant from the water's edge with the longer plot dimension perpendicular to the shoreline. The monospecific plots were situated so that they completely

consisted of the target vegetation; in mixed stands, the plot encompassed one *Avicennia* tree surrounded by *Spartina*. Each vegetation type per block was randomly assigned to a disturbance treatment or control (described below). All plots were instrumented with the rod surface elevation table-marker horizon (rSET-MH) system (described below), and measurements were conducted for one year prior to treatment application. Access to the plot interior without disturbance of the soil surface was achieved with a portable platform.

Disturbance treatments designed to kill aboveground plant parts were applied in March 2007. For *Avicennia* plots, all trees within the plot were treated with liquid nitrogen applied to the stem base using an insulation collar to confine and concentrate the freezing treatment. This approach caused mortality of the canopy distal to the freeze point. In a few cases, the freezing treatment was reapplied to kill any surviving branches. For *Spartina* plots, wrack was collected from a nearby marsh, deposited on the plot to cover the entire 3 x 5 m area, and held in place with bird netting. Both treatments were applied to Mixture plots. The undisturbed controls were not manipulated except for installation of rSET-MHs. No attempt was made to remove standing-dead material, and the vegetation was allowed to recover naturally.

Soils and vegetation

In February 2007, prior to treatment application, soil cores (2 cm diameter x 15 cm depth) were collected from the study site with a piston corer, dried to constant mass at 70°C, and weighed. Dry bulk density was calculated as the dry mass per volume (g cm^{-3}). Porewater was collected at the same time from experimental plots and analyzed for salinity, pH, and sulfide as described previously (McKee, 1993). Percent live cover in each plot was estimated visually, using a 0.25 m^2 quadrat, in April 2008.

Vertical accretion and surface elevation change

Rates of VA, root zone and sub-root zone movements, and SEC were determined with the rSET-MH system (Cahoon *et al.*, 2002; Lynch *et al.*, 2015). The rSET quantifies movements occurring

over different segments of the soil profile by measuring surface elevation relative to benchmarks at different depths (see https://www.pwrc.usgs.gov/set/theory.html for diagrams illustrating this method). A deep benchmark, which was driven to the point of refusal (ca. 15 m), provided a measure of the total movement over the entire soil profile. A portable measuring arm was attached to the deep benchmark in each of four fixed directions and leveled in both the horizontal and vertical planes. Nine fiberglass pins were lowered through the arm to the measurement surface, and pin extension above the arm was recorded to the nearest millimeter on each date (36 pins per rSET). Shallow benchmarks and marker horizons were established simultaneously with rSETs. A shallow benchmark, which consisted of 6-cm diameter aluminum pipe capped with an acrylic plate, was driven to a depth of 0.3 m (i.e., the root zone) along a fifth arm direction. On each measurement date, two pins were lowered from the arm to the top of the shallow benchmark. Pin heights on shallow benchmarks recorded expansion or contraction of the stratum below 0.3 m, whereas pins on the soil surface recorded total movement relative to the base of the deep benchmark. To measure accretion of sediment on the soil surface, three marker horizons (each ca. 0.25 m^2 in area) of white feldspar clay were placed on the soil surface at each plot. Thickness of the sediment deposited above the marker was determined by coring with a "mini-Macaulay" corer (custom fabrication, Nolan's, Lafayette, LA, USA), which cuts a core (2 cm diameter) without vertical compression. Baseline measurements were made in April, 2006, one month after rSET installation; subsequent measurements were made at 6-month intervals for 2.5 years, then annually for an additional 3 years.

Measurements conducted relative to marker horizons and benchmarks allowed partitioning of total vertical movement into accretion on the soil surface and sub-surface movement, which was further partitioned into root zone and sub-root zone movements. For consistency, all negative numbers indicate contraction of the stratum and positive numbers indicate expansion. Total subsurface movement was thus calculated by subtracting VA from SEC. Movement of shallow benchmarks directly recorded sub-root zone movement (below 0.3 m

depth). Root zone movement (0 to 0.3 m depth) was calculated by subtraction. An elevation

deficit was calculated for each plot by subtracting the mean sea-level trend (based on tide gauge

records) from the SEC rate. The long-term trend (1947 to 2017) was 9.09 mm yr^{-1}, and the trend

during the study period (2006 to 2012) was 14.4 mm yr^{-1} (NOAA Station 8761724 Grand Isle,

LA, USA; https://tidesonline.nos.noaa.gov). The tide gauge trend reflects the regional change in

ocean height and subsidence occurring beneath the tide gauge benchmark during the selected time

interval. As a check on the tide gauge method, an "accretion deficit or surplus" was estimated as

described in Jankowski *et al.* (2017) by subtracting a calculated rate of relative SLR (the sum of

regional SLR (Letetrel *et al.*, 2015); shallow subsidence (from rSET-MH); and deep subsidence

(estimated from GPS stations)) from VA (marker horizon). Deep subsidence was estimated based

on the linear relationship between subsidence (measured at 13 GPS stations) and latitude in the

MRD (Figure 4 in Jankowski *et al.*, 2017).

Marsh surface elevations were referenced to the North American Vertical Datum of 1988

(NAVD88) using real-time kinematic (RTK) global positioning system (GPS) connected to a

Global Navigation Satellite System (GNSS) (Trimble R10 and TSC3; Trimble, Sunnyvale, CA)

coupled with the Continuously Operating Reference Station (CORS) network GULFNet.

Measurements were made at each rSET benchmark and corrected to NAVD88 (System: UTM,

Zone: 15 North, Datum: WGS 1984, Geoid: 12A). Initial height of the marsh surface was

calculated in relation to NAVD88 by correcting for the vertical dimensions of the rSET apparatus

and pin heights. Elevation capital (relative position in tidal frame) was calculated for each plot as

the difference between elevation and mean water level. Mean water level (m NAVD88) at the

study site was estimated from hourly data (Coastal Information Management System (CIMS);

http://cims.coastal.louisiana.gov) recorded at a nearby gauge (~1 km away) maintained by

Louisiana's Coastwide Reference Monitoring System (CRMS station 0292; CPRA, 2015). The

elevation deficit and elevation capital for study plots were compared to other saline sites in the

MRD (n = 46) using publicly available records from CIMS. Data for each station (marsh

elevation (NAVD88), rSET record (2006 – 2017), and hourly water levels (2007 – 2016)) were downloaded and individually summarized.

Statistical analyses

To calculate elevation change over time at study plots, a linear model was fit to the data for each rSET pin separately to determine the slope of the relationship (i.e., rate of change). Problematic pin readings were omitted from analysis if they were identified as outliers (Mahalanobis distance) or if the pin was noted to rest on an obstruction (e.g., a plant shoot or aerial root) or in a deep depression (e.g., a crab burrow) (98 pin readings out of 4,752 total were excluded). Also, due to logistical problems, only one block of rSETs could be measured on the last sampling date; these data are presented but not included in the analysis of linear trends. Because accurate reading of marker horizons became increasingly difficult over time, only the first three years of VA data were analyzed. Rates of SEC, VA, and root zone and sub-root zone movements were averaged for each rSET plot (experimental unit). Effects of vegetation type and disturbance were assessed with Analysis of Variance (ANOVA) using a mixed model (fixed effects = vegetation, disturbance; random effect = block); post-hoc multiple comparisons were conducted with Tukey's HSD. Although Analysis of Covariance (ANCOVA) can be used to account for a potentially confounding variable such as initial plot elevation (Baustian *et al.*, 2012), our data failed to meet assumptions for ANCOVA (i.e., a linear relationship between covariate and dependent variable, homogeneity of regression slopes). The lack of a relationship between initial plot elevations and the response variables indicated that elevation differences had no systematic effect on rates of accretion or elevation change during the six-year study.

Bivariate relationships among variables were assessed with Pearson's correlation coefficient. Differences in the slope of the linear relationship due to species or disturbance effects were tested with ANCOVA (in this case, the homogeneity of regression slopes was being tested);

the lack of an interaction between the continuous variable and the categorical variable would support a null hypothesis that the linear slopes were similar. Statistical analyses were performed in JMP Pro 13.0 (SAS, 2016).

Results

Initial elevation (m NAVD88) of *Avicennia* plots was significantly higher than *Spartina* or Mixture plots ($P < 0.01$, Tukey's HSD), but there was no difference in elevation between disturbed and control plots (Table 1). Dry bulk density in control plots varied from 0.37 to 0.72, with an overall average of 0.54 g cm^{-3} (Table 1). Porewater properties measured prior to treatment application indicated no differences between control and disturbed plots (Table 1). Dry bulk density and porewater salinity differed with vegetation type, however. Bulk density was highest in *Avicennia* plots compared to Mixture ($P = 0.047$, Tukey's HSD) and *Spartina* ($P = 0.0053$, Tukey's HSD) plots. Salinity was also highest in *Avicennia* plots, but differed only from Mixture plots ($P = 0.043$, Tukey's HSD). Sulfide concentrations were high in some *Spartina* plots, but did not differ significantly with species (Table 1). Live cover averaged 29% in disturbed plots compared to 71% in undisturbed plots (main effect, $F_{1,10} = 15.09$, $P = 0.003$) and differed with vegetation type (*Avicennia* (72%), Mixture (53%), *Spartina* (26%)) (main effect, $F_{2,10} = 8.82$, $P = 0.006$). Lack of a statistical interaction between vegetation type and disturbance effects ($F_{2,10} = 0.89$, $P > 0.1$) indicated that the freezing and wrack burial treatments had similar effects on live cover of *Avicennia* and *Spartina*, respectively.

Rates of VA, SEC, and subsurface movements did not differ significantly among vegetation types or with disturbance treatment (Fig. 3, Table 2). None of the elevation change variables was correlated with percent live cover. SEC rate was significantly correlated with sub-root zone movement (Fig. 4c, $P < 0.001$) and with combined root zone and VA (Fig. 4d; $P < 0.0001$), but not with other individual or combined strata (Fig. 4a,b,e,f; $P > 0.05$). Together, VA

and root zone movement explained 80% of the variation in SEC. All but one of the 18 plots showed an elevation deficit (range = -7.7 to 1.6; mean = -4.2 mm yr^{-1}); however, neither vegetation type nor disturbance significantly affected the elevation deficit ($F_{2 \text{ or } 1,10}$ = 1.21 or 0.76, respectively; P > 0.05). Elevation capital of study plots varied from 0.032 to 0.210 m NAVD88 (mean = 0.129 m) and differed by vegetation type ($F_{2,10}$ = 20.84, P = 0.0003): *Avicennia* (0.190 ± .007 m) greater than Mixture (0.107 ±0.018 m) and *Spartina* (0.090 ±0.011 m) (P = 0.0014 and 0.0003, respectively; Tukey's HSD). By comparison, elevation deficit and elevation capital for other saline sites in the MRD (n = 46 CRMS stations) ranged, respectively, from -7.2 to 6.3 mm yr^{-1} (mean = -1.1 mm yr^{-1}) and from -0.104 to 0.157 m (mean = 0.018 m).

Discussion

Prior research comparing resistance of salt marshes and mangroves to SLR has produced conflicting data about how mangrove expansion might alter vulnerability of coastal wetlands to submergence. To assess relative vulnerability, several studies have compared rates of sediment accretion in salt marshes and mangroves (Rogers *et al.*, 2006; Perry & Mendelssohn, 2009; Comeaux *et al.*, 2012). Rogers *et al.* (2006), working in southeast Australia, found higher accretion rates in mangrove zones (5.0 mm yr^{-1}) compared to salt marsh (2.2 mm yr^{-1}). A study conducted along the Texas coast reported significantly greater sediment accumulation in one of three mangrove sites compared to marsh (Port Aransas site: 7.4 vs. 1.8 mm yr^{-1}, respectively; ^{137}Cs-1963 peak); however, at the other two sites there was no statistical difference in accretion rate between mangrove and marsh habitats (Comeaux, 2010; Comeaux *et al.*, 2012). These studies compared salt marsh and mangrove sites that were at different elevations and/or distances from the shoreline, which could affect sedimentation rates. Perry and Mendelssohn (2009) compared side-by-side stands of mangroves and salt marsh in Louisiana that were equidistant

from a tidal creek but at different elevations (relative elevation: +3.0 cm, mangrove; -3.5 cm, salt marsh). They found no difference in mangrove versus salt marsh accretion rates measured with three different methods: long-term (1963 to 2006) = 5.3 vs. 5.8 mm yr^{-1} (^{137}Cs 1963 peak, n = 1), medium-term (1 year) = 6.6 vs. 5.9 mm yr^{-1} (feldspar marker, n = 10), and short-term (seven sampling periods of 2-wk duration) = 0.22 vs. 0.30 g m^{-2} yr^{-1} (sediment trap, n = 10) (Perry & Mendelssohn, 2009). Our study, also conducted at equivalent spatial positions, found no significant difference in VA rates due to vegetation type, with or without disturbance (Table 2).

Comparison of sediment accretion rates, however, cannot fully assess relative vulnerability of these habitats to SLR because of subsurface movements (Cahoon *et al.*, 2006; Cahoon, 2015). Measurement of SEC relative to a stable benchmark provides a more accurate estimate because it integrates surface and subsurface movements. For example, although Rogers et al. (2006) found higher average rates of accretion at mangrove sites, subsidence rates were 4.8 times greater than at marsh sites. The net result was a rate of elevation gain at mangrove sites (0.6 mm yr^{-1}) that was arithmetically lower than at salt marsh sites (1.4 mm yr^{-1}). Thus, the benefit of higher accretion can be offset by subsurface compaction or other processes, leading to a lowering of the soil surface. Another scenario is that accretion rates might be similar in the two habitats (Table 2), but different subsidence rates would mean that one habitat was submerging faster than the other. We found, however, that root zone and sub-root zone movements were similar in *Spartina*, Mixture, and *Avicennia* plots, as well as in control and disturbed plots (Table 2). Thus, comparable rates of elevation gain observed in the experimental plots reflected similar rates of both surface and subsurface movements.

Effect of vegetation type

One way that plants can affect elevation dynamics is by influencing sediment deposition on the soil surface. Density and morphology of aboveground plant structures may modify sediment accretion by reducing water velocities (Scoffin, 1970) or alternatively by increasing turbulence

(Spenceley, 1977), which, in turn, affects particle capture or settlement (Mudd *et al.*, 2010). Despite differences among vegetation types in height and percent cover, VA rates were similar (Table 2), which suggests two possibilities: (1) the vegetation had no effect on deposition and trapping of sediments or (2) *Avicennia* and *Spartina* plant structures affected sedimentation in a similar way. The first option is less likely since several studies have shown that sediment accretion increases with *Avicennia* pneumatophore density (Bird, 1986; Young & Edward Harvey, 1996) or *S. alterniflora* stem density (Mudd *et al.*, 2010). The more likely explanation is that mangrove and salt marsh vegetation had comparable effects on sedimentation. Densities of plant structures in Louisiana salt marsh and mangrove stands are, in fact, similar: *S. alterniflora* (364 culms m^{-2}) and *A. germinans* (450 pneumatophores m^{-2}) (Eady, 2007). Comparable stem densities may explain the similarity in VA rates found in this (Table 2) and other studies involving these species (Perry & Mendelssohn, 2009).

Plants also influence SEC through contribution of root biomass to soil volume expansion, as shown in manipulative experiments (McKee *et al.*, 2007; Cherry *et al.*, 2009; Langley *et al.*, 2009). Those studies were conducted in peat-forming habitats where changes in production of refractory root matter had a substantial effect on upward expansion of the soil surface. For example, phosphorus fertilization of subsiding red mangrove stands in Belize increased root accumulation 8- to 10-fold, which led to dramatic gains in elevation (McKee *et al.*, 2007). Although root accumulation was not determined in our experimental plots, a study conducted nearby found no significant difference in root production between *A. germinans* (346 g m^{-2} yr^{-1}) and *S. alterniflora* (436 g m^{-2} yr^{-1}) (Perry & Mendelssohn, 2009). Similar rates of root matter accumulation may explain why movement in the root zone did not differ with vegetation type in our study (Table 2).

The third way that plants can influence elevation dynamics is by altering soil shear strength and resistance to compaction or erosion. Soil shear strength increases with the presence of live roots and rhizomes, which form a strong matrix in the upper soil layers. For example,

shear strength in an oligohaline marsh decreased with depth as live root biomass declined (Graham & Mendelssohn, 2014). Shear strength of mangrove soils can vary across zones of differing root productivity (Cahoon *et al.*, 2003) or with the presence of algal mats growing on the soil surface (McKee, 2011). In salt marshes dominated by *S. alterniflora*, soil shear strength varied from 11 kPa at the surface to 4.5 kPa at 20 to 50 cm depths (Turner, 2011). Comeaux (2010) also found that soil strength in Texas salt marsh-mangrove stands varied over depth, but did not find significant differences between mangrove and marsh habitats. Soil strength was not measured in our experimental plots, but the similarity in subsurface movement among *Spartina*, *Avicennia,* and Mixture plots (Table 2) indicates that resistance to compaction was not greatly affected by vegetation type.

Similarity in accretion rate (Perry & Mendelssohn, 2009; Table 2, this study), belowground root production (Perry & Mendelssohn, 2009), and soil strength (Comeaux, 2010) may explain why SEC did not differ with mangrove or marsh species (Fig. 3b). However, this result may be unique to this particular combination of species, sedimentary setting, and spatial position on creek banks. Other work has shown effects of salt marsh vegetation on elevation of interior marshes in the MRD. For example, the study by Baustian et al. (2012), which found that *S. alterniflora* presence significantly increased VA and SEC rates, was conducted in the marsh interior 25 to 75 m from a waterway. Plants may have a greater effect on marsh elevation in interior sites receiving less sediment or where the substrate has a higher organic content and potential for collapse (Delaune *et al.*, 1994; Day *et al.*, 2011). Thus, mangrove and salt marsh stands in the wetland interior may behave differently from those on creek banks. Also, our findings are relevant only for the two species studied in the MRD. Co-occurring salt marshes and mangroves in other geographic areas composed of different species may display differences in one or more plant processes influencing elevation dynamics.

A final point about interpretation of vegetation effects concerns the potential confounding effect of initial elevation, which could not be controlled in this study, either experimentally or

statistically (see Methods). Elevation of the marsh surface relative to sea level determines accommodation space (i.e., the space available for sediment accumulation) and thus could directly affect accretion of sediment. Elevation also influences depth and duration of flooding and edaphic properties (Table 1), which may, in turn, alter vegetation contributions to surface and subsurface movements. These biophysical properties and processes are inextricably linked, making it difficult to ascribe cause and effect. However, we found no relationship between initial elevation and rates of accretion ($r = 0.20$, $P = 0.423$) or elevation change ($r = 0.37$, $P = 0.132$), which suggests no systematic influence of elevation. While we cannot know how the experimental plots would have compared had salt marsh, mixed, and mangrove starting elevations been identical, we can say that, despite differences in elevation, they were accreting sediment and building vertically at similar rates during the six-year study (Fig. 3b, Table 2). Differences in elevation, however, do play a role in determining relative vulnerability of mangrove and salt marsh areas to sea-level rise, and this effect is discussed in more detail below.

Effect of disturbance

The lack of a disturbance effect on SEC in this salt marsh-mangrove community (Fig. 3a, Table 2) is informative because it contrasts with a growing body of experimental work showing that manipulation of the vegetation can alter wetland elevation trajectories (Morris *et al.*, 2002; McKee *et al.*, 2007; Langley *et al.*, 2009; McKee, 2011; Baustian *et al.*, 2012). Although much of that work involved increases in SEC rates caused by experimental increases in shoot density or root production, a few cases have shown that disturbance of existing vegetation can have a negative effect on elevation. Mortality of mangroves due to hurricanes or human activities, for example, can lead to elevation loss (Cahoon *et al.*, 2003; Stokes & Harris, 2015) or lowered resistance to erosion (McKee & Vervaeke, 2009). In mangrove systems in Honduras and Belize, the presence of mangrove roots was associated with high shear strength in both organic and mineral soils; disturbance of the vegetation or soils increased subsidence rates and decreased

erosion resistance (McKee & McGinnis, 2002; Cahoon *et al.*, 2003; McKee & Vervaeke, 2009). In those cases, elevation loss was attributed to one or more factors: collapse of the living root matrix, a change in aboveground structures promoting sedimentation, or a decrease in organic matter contributions to soil volume. One study, however, found that experimental reduction of mangrove cover led to increased sediment accretion, but this outcome may have been caused by erosion along the shoreward edge of plots and transport of sediment to plot interiors (Guo *et al.*, 2017).

Another possibility exists in which disturbance of the vegetation has little or no effect on elevation dynamics because biotic influences are overshadowed by physical processes of inorganic sedimentation, erosion, and auto-compaction. Such may be the case in this study (Fig. 3, Table 2). This explanation is supported by the fact that disturbance had no effect on VA or root zone movement in both mangrove and salt marsh plots (Table 2). Also, significant differences in live cover across vegetation types had no influence on SEC (Fig. 3, Table 2). A larger disturbed area, however, may have produced a different result. Plot size was relatively small (15 m^2), in part to allow practicable application of disturbance treatments, but also to match natural areas of small wrack deposits or freeze damage. Small patches of damage may recover more quickly than larger ones and before sediment accretion or subsidence can be affected. A small, disturbed patch may be quickly repaired through root and rhizome ingrowth from surrounding vegetation. Also, even if no longer alive, the root system in the disturbed plots may have continued to sustain soil strength and resistance to compaction, as found in a mangrove forest in Honduras killed by a hurricane (Cahoon *et al.*, 2003). Persistence of standing-dead structures aboveground (grass culms, mangrove pneumatophores) could have continued to influence sedimentation in a way similar to live structures until the vegetation recovered. Plot size, however, likely had little influence on detection of differences among vegetation types since the rSET measurement area (ca. 2 m diameter) was the same across plots. Also, this measurement area is consistent with other

studies using the rod-type SET to compare vegetation (Cahoon *et al.*, 2003; McKee *et al.*, 2007; Langley *et al.*, 2009; McKee & Cherry, 2009; Baustian *et al.*, 2012).

Vulnerability to sea-level rise

To assess vulnerability of the salt marsh-mangrove community to SLR, SEC rates were compared to the sea-level trend recorded at a local tide gauge. This calculation essentially quantifies whether sea level is rising, is unchanging, or is falling in relation to the wetland surface (Cahoon, 2015). The tide gauge trend reflects sea surface movement and deep land movement below the reference benchmark, but not shallow subsidence occurring in the wetland (Cahoon, 2015). However, comparison of the SEC rate (rather than VA) with the tide gauge trend automatically takes shallow subsidence in the wetland into account. Comparison of the long-term trend at the tide gauge (9 mm yr^{-1}) with the SEC rate at our study site (5 mm yr^{-1}) yielded an average elevation deficit of 4 ± 1 mm yr^{-1}, indicating that sea level was rising faster than the wetland was building vertically (two-tailed Student's t-test$_{(df=17)}$ = 6.8, $P < 0.0001$). Several factors potentially confound this interpretation, however (Cahoon, 2015). Distance between the rSET and the tide gauge can compromise the relevance of the calculation, although in this case the two sites were within the same deltaic setting and only 30 km apart. Another consideration is the different record lengths for the two measures. A direct comparison of the wetland elevation trend (~5 years) with the long-term record at a tide gauge (70 years) assumes that the sea-level trend during the elevation study is similar to the historic trend, which was not the case. The sea-level trend during the study interval was 14 mm yr^{-1}, yielding an elevation deficit of 9 ± 1 mm yr^{-1}. An alternative approach is to compare the VA rate (11 mm yr^{-1}) with a calculated rate of relative SLR (the sum of shallow subsidence from rSET-MH (6 mm yr^{-1}), deep subsidence estimated from GPS stations (6 mm yr^{-1}), and regional SLR (2 mm yr^{-1}) = 14 mm yr^{-1}) (as in Jankowski *et al.*, 2017)). That calculation yields a deficit of 3 ± 1 mm yr^{-1}, which is lower than that based on the tide gauge record. The disagreement among estimates is due to different sources

of off-site data used in the calculations (i.e., tide gauges or GPS stations), which may or may not accurately reflect what rate of relative SLR the wetland is actually experiencing. In any case, the results show that the salt marsh-mangrove community was not keeping pace with either recent or long-term rates of relative SLR and was experiencing elevation deficits of at least 3 mm yr^{-1}.

Coastal wetlands in the MRD with elevation deficits greater than 2 mm yr^{-1} are considered to be highly vulnerable to submergence (Jankowski *et al.*, 2017). The elevation deficits (calculated based on the long-term tide gauge trend) for study plots were variable, ranging from -7.7 to 1.6 mm yr^{-1}. Although these values fall within the range for saline wetlands in the MRD (-7.2 to 6.3 mm yr^{-1}, n = 46), a majority of study plots (72%) had an elevation deficit greater than 2 mm yr^{-1}. Only 41% of CRMS sites had deficits exceeding 2 mm yr^{-1}. The differences in elevation deficit within and among sites in the MRD reflect spatial variation in VA and sub-surface movements. VA varied substantially across study plots from 5 to 21 mm yr^{-1}, and total subsurface movement varied from -17 to 1 mm yr^{-1}. The root zone accounted for 57%, on average, of subsurface movement. In fact, about 80% of the variation in SEC rates and, hence elevation deficit, across the salt marsh-mangrove plots was attributable to the combination of accretion and root zone movement ($P < 0.0001$) (Fig. 4d). This linear relationship was consistent across vegetation types (ANCOVA testing different slopes: $F_{1,12} = 2.19$, $P > 0.05$) and disturbance treatments ($F_{1,14} = 0.09$, $P > 0.05$). Thus, despite no treatment or species effects on elevation dynamics, our results agree with other manipulative field experiments showing the strong influence of the root zone and sediment accretion on elevation gain or loss in coastal wetlands (McKee *et al.*, 2007; Langley *et al.*, 2009; Mudd *et al.*, 2010; McKee, 2011; Baustian *et al.*, 2012).

In addition to the elevation deficit, the height of the wetland surface in relation to local sea level must also be considered in assessing vulnerability to sea-level rise. Wetlands positioned higher in the tidal frame have more elevation capital (i.e., are less vulnerable) than those positioned lower. A plot combining elevation capital and elevation deficit allows better

visualization of relative vulnerability of wetland sites to submergence (Fig. 5). Those sites with high elevation deficits and low elevation capital would be most vulnerable, and those with low deficits and high capital would be least vulnerable.

Most of the salt marsh-mangrove plots showed elevation deficits but were positioned high in the tidal frame, which means they were surviving on elevation capital. The study plots were situated higher in the tidal frame (0.129 ± 0.014 m NAVD88, n = 18) than CRMS sites (0.017 ± 0.009 m NAVD88, n = 46) ($F_{1,62}$ = 43.8, P < 0.0001) (Fig. 5). The greater elevation capital of study plots may be attributable to their creek bank position where natural elevations tend to be 5 to 10 cm higher than in the marsh interior (DeLaune *et al.*, 1983). Also, elevations of *A. germinans* stands studied in Louisiana and Texas were 4 to 10 cm higher than salt marsh elevations (Table 1, this study; Perry & Mendelssohn, 2009; Comeaux *et al.*, 2012; Henry & Twilley, 2013) and, consequently, had more elevation capital. Given no significant difference in elevation deficit among vegetation types, the greater elevation capital of *Avicennia* plots suggests they will survive longer than *Spartina* or Mixture plots. However, spatial and temporal variability in both wetland elevation and sea-level trends makes predictions difficult. What can be concluded is that a shift from salt marsh to mangrove vegetation or temporary reductions in plant cover of either species may not alter the capacity of this wetland to keep up with relative SLR, whatever the actual rates may be.

Wetland elevation: cause or consequence of vegetation?

If mangroves and salt marshes accrete sediment and build vertically at equivalent rates (Fig. 3b, Table 2), why are mangroves found at higher elevations in Louisiana and Texas (Table 1, this study; Perry & Mendelssohn, 2009; Comeaux *et al.*, 2012; Henry & Twilley, 2013)? This question is not easy to answer because elevation could be the cause or the consequence of the vegetation. Higher elevations in *Avicennia*-dominated areas might occur because of faster

sediment accretion or greater organic matter accumulation, but side-by-side comparisons with salt marsh do not support this explanation (Table 2) (Perry & Mendelssohn, 2009; Yando *et al.*, 2016). Also, the tendency of mangrove stands in the MRD to initiate along creek banks (Fig. 1b, Fig. 2a) suggests another explanation. Because mangrove propagules are buoyant, they can settle and take root only where the soil surface remains unflooded for a few days (Rabinowitz, 1978). The naturally higher elevations of creek banks reduce depth and duration of flooding, allowing mangroves to establish more readily than in the lower elevation marsh interior. More *Avicennia* propagules are retained at higher elevations on creek banks and also suffer less predation and decay (Patterson *et al.*, 1997). In addition, the propensity for wrack to collect on creek banks may aid mangrove establishment by trapping propagules and creating bare areas in the salt marsh (Fig. 2c-e, Fig. S1). Thus, *Avicennia*-dominated stands in the MRD may be associated with higher elevations because conditions are more conducive to mangrove establishment. Furthermore, in Australia, mangrove stands typically occur at lower elevations than salt marsh (Rogers, 2004), a pattern opposite to that reported in Louisiana and Texas. If differences in elevation do reflect vegetation influences, then the effect is not the same in all geographic regions where salt marshes and mangroves co-exist. A key factor may be how much the vegetation types differ in structural and functional features that influence elevation dynamics (Yando *et al.*, 2016). However, because mangroves and salt marshes are often found at different elevations or at different distances from the shoreline, their respective capacities to keep pace with SLR may be particularly difficult to ascertain—unless those confounding factors are addressed in the experimental design (e.g., all plots are equidistant from the shoreline; Perry & Mendelssohn, 2009; this study) or statistical analysis (e.g., ANCOVA with initial elevation as covariate; Baustian *et al.*, 2012).

Implications for other coastal wetlands

Future stewardship of coastal wetlands requires conservation and restoration plans that not only anticipate changes in climate, but that incorporate information about how climate-driven shifts in dominant vegetation will affect the capacity of the system to accommodate sea-level rise. To accomplish this objective, we seek generalizations that can guide and facilitate decision-making. Some investigators have hypothesized that mangrove expansion at climatic boundaries will decrease vulnerability of coastlines to SLR (Rogers *et al.*, 2006; Comeaux *et al.*, 2012; Saintilan *et al.*, 2014). These predictions may be accurate—for their respective environmental settings and vegetative compositions. Our study demonstrates another possibility, which is that mangrove replacement of salt marsh may not lead to a significant change in capacity to accommodate rising sea level (although other structural and functional features may change (Kelleway *et al.*, 2017)). In some geographic locations, co-occurring species may not differ enough to alter elevation dynamics. In other settings, effects of the vegetation on elevation may be overshadowed by physical factors, such as tide range (Kirwan & Guntenspergen, 2010; Lovelock *et al.*, 2015), groundwater flux (Rogers & Saintilan, 2009; Cahoon *et al.*, 2011), subsidence (Jankowski *et al.*, 2017), or storm-driven sediment pulses (McKee & Cherry, 2009; Whelan *et al.*, 2009). In addition, disturbances to the vegetation may not necessarily lead to elevation loss—for example, if vegetative recovery occurs before elevation-sustaining processes are affected. However, as this study has shown, physical factors affecting elevation trajectories (sediment accretion, shallow subsidence) vary spatially, even along a single tidal creek. Thus, examination of the influence of vegetation shifts on vulnerability to SLR must be conducted in a way to avoid or account for these potentially confounding factors.

Acknowledgements

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Table 1. Summary of pre-treatment soil and porewater properties and initial elevation measured in plots containing different vegetation types (*Avicennia*, Mixture, *Spartina*) and assigned to disturbance treatments (control, disturbed). Values are the mean ± SE (n = 6 or 9 for vegetation type or disturbance, respectively). ANOVA results are given below ($P \leq 0.05$*, 0.01**, 0.001***; ns = not significant; df = 1, 12 (disturbance), 2, 12 (vegetation), 2, 12 (interaction); nd = not determined).

	Bulk density (g cm^{-3})	pH	Salinity	Sulfide (mM)	Elevation (m NAVD88)
Control	0.54 ± 0.04	6.7 ± 0.1	28 ± 2	1.80 ± 0.93	0.272 ± 0.020
Disturbed	nd	6.8 ± 0.2	27 ± 2	2.18 ± 1.75	0.277 ± 0.017
Avicennia	0.67 ± 0.03	6.9 ± 0.2	32 ± 3	0.21 ± 0.20	0.336 ± 0.007
Mixture	0.53 ± 0.03	6.7 ± 0.1	24 ± 1	0.55 ± 0.15	0.253 ± 0.018
Spartina	0.41 ± 0.02	6.7 ± 0.1	26 ± 1	5.20 ± 2.50	0.236 ± 0.011
ANOVA (F-ratio):					
Disturbance	-	0.33ns	0.05ns	0.05ns	0.14ns
Vegetation	21.02***	0.86ns	4.49*	3.58ns	20.8***
Dist. x Veg.	-	0.81ns	0.02ns	0.14ns	0.30ns

Table 2. Summary of surface elevation change data (mm yr^{-1}) in plots containing different vegetation types (*Avicennia*, Mixture, *Spartina*) and assigned to disturbance treatments (control, disturbed). Values represent net movements relative to benchmarks: marker horizon (vertical accretion); shallow benchmark at 0.3 m (root zone); and deep benchmark at ~15 m (SEC, sub-root zone, and total subsurface). Data are the mean ± 1 SE (n = 6 or 9 for vegetation type or disturbance, respectively); observation interval = 3 yr (accretion, root zone, and total subsurface movement) or 4.75 yr (elevation change, sub-root zone). Negative or positive values indicate contraction or expansion of the stratum. ANOVA results are given below (ns = not significant; df = 1, 10 (disturbance) or 2, 10 (vegetation and interaction)).

	Elevation Change	Vertical Accretion	Root Zone	Sub-Root Zone	Total Subsurface
Control	5.4 ± 0.9	10.0 ± 1.1	-2.6 ± 0.7	-2.0 ± 0.3	-4.6 ± 0.8
Disturbed	4.4 ± 0.7	12.4 ± 1.6	-5.5 ± 1.9	-2.5 ± 0.4	-8.0 ± 2.0
Avicennia	4.1 ± 0.4	11.4 ± 2.4	-4.4 ± 2.5	-2.9 ± 0.3	-7.3 ± 2.3
Mixture	6.1 ± 1.3	11.9 ± 1.7	-4.2 ± 2.1	-1.6 ± 0.6	-5.8 ± 2.5
Spartina	4.6 ± 0.9	10.4 ± 1.2	-3.6 ± 1.1	-2.2 ± 0.3	-5.8 ± 1.1

ANOVA (F-ratio):

	Elevation Change	Vertical Accretion	Root Zone	Sub-Root Zone	Total Subsurface
Disturbance	0.76ns	1.12ns	1.49ns	0.68ns	1.90ns
Vegetation	1.21ns	0.14ns	0.04ns	1.81ns	0.16ns
Dist. x Veg.	1.09ns	0.27ns	0.04ns	0.01ns	0.04ns

Figure 1. (a) Location of the study site in the Mississippi River Delta northwest of Port Fourchon, Louisiana, USA. (b) Experimental plots were established along a natural tidal creek in monospecific stands of *Avicennia germinans* or *Spartina alterniflora*, and in stands containing

both species. Dark vegetation on the creek banks is mangrove (*A. germinans*), and lighter vegetation is salt marsh (*S. alterniflora*). Images by NASA/JPL (North America inset) and Google Earth Pro (V 7.3.0.3832; Landsat/Copernicus; December 30, 2012; eye alt 214 km (a); November 14, 2012; eye alt 377 m (b)).

Figure 2. Views of the salt marsh-mangrove community in the Mississippi River Delta. (a) aerial view of a mangrove stand (dark vegetation along creek) adjacent to landward salt marsh, (b) ground view of *Avicennia germinans* (black mangrove), (c-d) wrack (plant debris) and resultant bare patch created by *Spartina alterniflora* mortality (arrows indicate reference points), (e) mangrove propagules establishing in a bare patch created by wrack (note pneumatophores that were deformed by wrack burial) and (f) freeze-damaged black mangroves. Photographs by K.L. McKee.

Figure 3. Time-course change in surface elevation grouped by (a) disturbance (Control, Disturbed) or (b) vegetation type (*Avicennia germinans*, *Spartina alterniflora*, Mixture (both species)). Disturbance treatments were applied to *Avicennia* (freezing), *Spartina* (wrack burial) and Mixture (freezing and wrack) at 1 year. Values are the mean ± SE (n = 9 or 6 for disturbance treatment or vegetation type, respectively, years 1–5; n = 3 or 2, year 6).

Figure 4. Bivariate relationship between elevation change rate and movements in different strata: (a) vertical accretion (above marker horizon), (b) root zone, (c) sub-root zone, (d) accretion and root zone, (e) root and sub-root zone, (f) accretion and sub-root zone. Pearson's correlation coefficient (r) indicates linear fit if significant (ns = not significant). Symbol shape indicates species: *Avicennia* (triangle), Mixture (diamond), *Spartina* (square), and symbol fill indicates treatment: Control (open), Disturbed (closed).

Figure 5. Relative vulnerability to sea-level rise of saline vegetation types in the Mississippi River Delta. Vegetation types in experimental plots (n = 18) were: *Avicennia germinans*

(*Avicennia*) *Spartina alterniflora* (*Spartina*), and both species (Mixture). Data for additional saline wetland sites (n = 46), dominated by *S. alterniflora*, are from Louisiana's Coastwide Reference Monitoring System (CRMS) (CPRA, 2015). Elevation deficit or surplus was calculated as the difference between rates of surface elevation change (SEC) and the long-term sea-level trend at a local tide gauge (9.09 mm yr^{-1}). The vertical line indicates where SEC equals the sea-level trend. Elevation capital (relative position of the wetland in the tidal frame) was calculated as the difference between the elevation of the wetland surface and mean water level, both related to a common datum; the horizontal line indicates where the marsh elevation equals the mean water level.