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Michael J. Osland

Christopher A. Gabler
The University of Texas Rio Grande Valley

James B. Grace

Richard H. Day

Meagan L. McCoy

See next page for additional authors

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Part of the Earth Sciences Commons, Environmental Sciences Commons, and the Marine Biology Commons

Authors

Michael J. Osland, Christopher A. Gabler, James B. Grace, Richard H. Day, Meagan L. McCoy, Jennie L. McLeod, Andrew S. From, NIcholas M. Enwright, Laura C. Feher, and Camille L. Stagg

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Climate and plant controls on soil organic matter in coastal wetlands

Michael J. Osland[1] iD | Christopher A. Gabler[2] iD | James B. Grace[1] iD | Richard H. Day[1] iD | Meagan L. McCoy[3] iD | Jennie L. McLeod[3] iD | Andrew S. From[1] iD | Nicholas M. Enwright[1] iD | Laura C. Feher[1] iD | Camille L. Stagg[1] iD | Stephen B. Hartley[1] iD

[1]Wetland and Aquatic Research Center, U.S. Geological Survey, Lafayette, Louisiana

[2]School of Earth, Environmental, and Marine Sciences, The University of Texas Rio Grande Valley, Brownsville, Texas

[3]University of Louisiana at Lafayette, Lafayette, Louisiana

Correspondence
Michael J. Osland, Wetland and Aquatic Research Center, U.S. Geological Survey, Lafayette, LA.
Email: mosland@usgs.gov

Abstract

Coastal wetlands are among the most productive and carbon-rich ecosystems on Earth. Long-term carbon storage in coastal wetlands occurs primarily belowground as soil organic matter (SOM). In addition to serving as a carbon sink, SOM influences wetland ecosystem structure, function, and stability. To anticipate and mitigate the effects of climate change, there is a need to advance understanding of environmental controls on wetland SOM. Here, we investigated the influence of four soil formation factors: climate, biota, parent materials, and topography. Along the northern Gulf of Mexico, we collected wetland plant and soil data across elevation and zonation gradients within 10 estuaries that span broad temperature and precipitation gradients. Our results highlight the importance of climate–plant controls and indicate that the influence of elevation is scale and location dependent. Coastal wetland plants are sensitive to climate change; small changes in temperature or precipitation can transform coastal wetland plant communities. Across the region, SOM was greatest in mangrove forests and in salt marshes dominated by graminoid plants. SOM was lower in salt flats that lacked vascular plants and in salt marshes dominated by succulent plants. We quantified strong relationships between precipitation, salinity, plant productivity, and SOM. Low precipitation leads to high salinity, which limits plant productivity and appears to constrain SOM accumulation. Our analyses use data from the Gulf of Mexico, but our results can be related to coastal wetlands across the globe and provide a foundation for predicting the ecological effects of future reductions in precipitation and freshwater availability. Coastal wetlands provide many ecosystem services that are SOM dependent and highly vulnerable to climate change. Collectively, our results indicate that future changes in SOM and plant productivity, regulated by cascading effects of precipitation on freshwater availability and salinity, could impact wetland stability and affect the supply of some wetland ecosystem services.

KEYWORDS
carbon, climate change, coastal wetland, mangrove, plant productivity, precipitation, salinity, salt marsh, soil organic matter, temperature

1 | INTRODUCTION

Soils contain the largest terrestrial carbon pool on Earth and store more carbon than the global vegetation and atmospheric carbon pools combined (Houghton, 2007; Jackson et al., 2017; Jobbágy & Jackson, 2000; Schlesinger & Bernhardt, 2013). To anticipate and mitigate the effects of climate change, there is a pressing need to advance understanding of the fate and storage of carbon in soil organic matter (SOM). Clarifying the factors that control SOM is particularly important for ecosystems that are carbon rich, climate sensitive, and have the potential for large carbon fluxes to and from the atmosphere (Atwood et al., 2017; Howard, Hoyt, Isensee, Telszewski, & Pidgeon, 2014; Lovelock, Atwood, et al., 2017; Rovai et al., 2018; Twilley, Chen, & Hargis, 1992). Mangrove forests and salt marshes are coastal wetland ecosystems that support highly productive vascular plant communities, and a large amount of the organic matter produced by these plants accumulates belowground as SOM due to the presence of abiotic conditions that constrain decomposition (Chmura, Anisfeld, Cahoon, & Lynch, 2003; Mendelssohn & Morris, 2000). Furthermore, coastal wetlands accrete sediment and organic matter as sea-level rises (McKee, Cahoon, & Feller, 2007; Reed, 1995), providing continuously increasing accommodation space for SOM accumulation and burial. As a result, the belowground carbon stocks and carbon burial rates in coastal wetland ecosystems are among the highest on Earth (Donato et al., 2011; Mcleod et al., 2011). The effects of climate change on wetland soil carbon have been of great concern, partly due to the potential for feedbacks that could alter carbon fluxes to the atmosphere and amplify climate change impacts (Bradford et al., 2016; Chapin, Sturm, & Serreze, 2005; Kirwan & Mudd, 2012; Wang, Richardson, & Ho, 2015).

Knowledge of the effects of climate change on SOM is particularly important in ecosystems like coastal wetlands, where relatively small changes in climate can lead to ecosystem loss or trigger landscape-scale changes in ecosystem structure and function (i.e., ecological regime shifts sensu Scheffer, Carpenter, Foley, Folke, and Walker (2001)). In coastal wetlands, foundation plant species play an important functional role; for example, mangrove and salt marsh plants create habitat, modulate ecosystem functions, and support entire ecological communities (Bruno & Bertness, 2001; Ellison et al., 2005). These foundation plant species also support many ecosystem goods and services (Barbier et al., 2011; Ewel, Twilley, & Ong, 1998). Foundation plant species contribute to coastal wetland stability in the face of rising sea levels through biogeomorphic feedbacks between inundation, plant growth, SOM accumulation, and sedimentation (Kirwan & Megonigal, 2013; Krauss et al., 2014; McKee & Vervaeke, 2018; Morris, Sundareshwar, Nietch, Kjerfve, & Cahoon, 2002). However, coastal wetland foundation species are highly sensitive to ecological regime shifts induced by climate change (Gabler et al., 2017; Osland et al., 2016a). For example, near the transition between tropical and temperate climates, warming temperatures can lead to mangrove forest expansion at the expense of salt marsh ecosystems (Cavanaugh et al., 2014; Osland, Enwright, Day, & Doyle,

2013; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). Likewise, near the transition between arid and humid ecosystems, changes in precipitation and salinity can trigger large changes in the coverage and performance of foundation plant species; for example, drought can lead to mangrove contraction, salt marsh contraction, and/or salt flat expansion (Duke et al., 2017; Dunton, Hardegree, & Whitledge, 2001; Eslami-Andargoli, Dale, Sipe, & Chaseling, 2009; Lovelock, Feller, Reef, Hickey, & Ball, 2017; McKee, Mendelssohn, & Materne, 2004).

Our understanding of climatic controls on coastal wetland plant communities and aboveground ecosystem properties has been improving rapidly in recent years (Feher et al., 2017; Gabler et al., 2017; Osland, Feher, et al., 2017); however, there is still much to learn about the influence of climatic drivers on soil and belowground ecosystem properties (Doughty et al., 2016; Henry & Twilley, 2013; Kelleway et al., 2017; Perry & Mendelssohn, 2009; Simpson, Osborne, Duckett, & Feller, 2017). In Figure 1, we illustrate the effects of climate on coastal wetland plant communities in the northern Gulf of Mexico and show with question marks that the corresponding effects on soil properties are not fully understood. In Figure 2, we present hypotheses from the terrestrial and coastal wetland literature regarding the influence of climate on carbon-related soil properties. In terrestrial ecosystems, there can be positive relationships between mean annual precipitation and soil organic carbon (Burke et al., 1989; Jobbágy & Jackson, 2000; Klopfenstein, Hirmas, & Johnson, 2015; Luo, Feng, Luo, Baldock, & Wang, 2017; Waldrop et al., 2017) and negative relationships between mean annual temperature and soil organic carbon (Fissore et al., 2008;
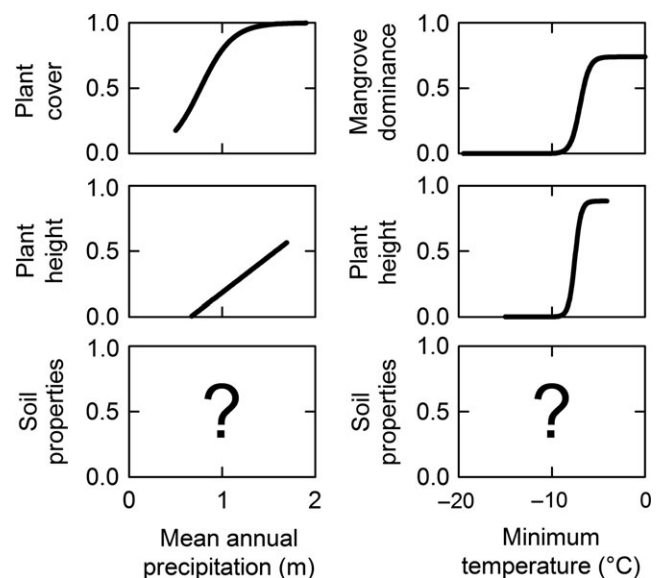

FIGURE 1 Although the influence of climate on coastal wetland vegetation has been quantified (upper and middle panels), the corresponding effects of climate and vegetation on soil properties have not been quantified (see lower panel question marks). Data in upper and middle panels are from the northern Gulf of Mexico (Gabler et al., 2017; Osland et al., 2013, 2014)
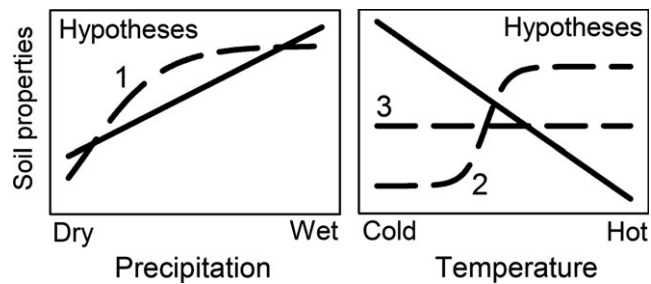
FIGURE 2 Alternative hypotheses regarding the influence of climate on carbon (C)-related soil properties. Solid lines represent relationships from terrestrial ecosystems. Dashed lines represent hypotheses from the coastal wetland literature: (1) ↑↓ precipitation ▬ nonlinear ↑↓ plant coverage, nonlinear ↑↓ plant productivity, nonlinear ↑↓ aboveground C, nonlinear ↑↓ belowground C, respectively; (2) ↑ temperature ▬ mangrove replacement of marsh, nonlinear ↑ aboveground C, nonlinear ↑ belowground C; and (3) ↑ temperature ▬ mangrove replacement of marsh, nonlinear ↑ aboveground C, no change in belowground C

Schimel et al., 1994; see solid lines in Figure 2; left and right panel respectively). However, in coastal wetlands, there are several alternative hypotheses regarding the influence of climatic drivers on carbon-related soil properties (see caption and dashed lines in Figure 2). Analyses of literature-derived data indicate that there may be no relationship between temperature and soil carbon density or soil carbon accumulation in coastal wetlands (Chmura et al., 2003; Feher et al., 2017; Figure 2, straight dashed line in right panel) and that there may be a positive relationship between precipitation and coastal wetland belowground carbon stocks (Sanders et al., 2016; Figure 2, dashed line in left panel). However, the absence of field-based data collected systematically and strategically across regional climatic gradients has hindered our ability to test these hypotheses and advance understanding of the influence of climatic drivers on soil carbon storage and cycling in coastal wetlands (Feher et al., 2017; Osland et al., 2016a).

In a seminal communication regarding soil development, Jenny (1941) identified five critical factors that control soil formation in all ecosystems: climate, biota, topography, parent materials, and time. Here, we evaluate an integrative hypothesis for how four of these soil formation factors might influence SOM in coastal wetlands (Figure 3). Time was not included in our analyses due to the lack of temporal data. However, coastal wetlands are dynamic and ephemeral ecosystems that must adjust to sea-level fluctuations via vertical or horizontal movement across the landscape. As a result, soil properties at the wetland surface are often indicative of recent conditions, and soil organic matter development can occur very rapidly in these ecosystems (i.e., much faster than in terrestrial ecosystems; Craft, Reader, Sacco, & Broome, 1999; Osland et al., 2012; Walcker et al., 2018).

Based upon the literature and prior analyses (Chmura et al., 2003; Feher et al., 2017; Yando et al., 2016), we hypothesized that, in our study area, the influence of temperature on SOM in coastal wetlands is small or not significant (Figure 2, straight dashed line in

right panel), though we include the potential for a temperature effect in our models for evaluation purposes. We hypothesized that there would be strong direct and indirect effects of precipitation, salinity, and plant productivity on SOM (Feher et al., 2017; Gabler et al., 2017; Osland, Enwright, & Stagg, 2014; Yando et al., 2016; Figure 2, nonlinear dashed line in left panel). More specifically, we expected that productive communities (especially mangrove forests and graminoid-dominated salt marshes) would have higher SOM than less productive ones (especially salt flats without vascular plants or salt marshes dominated by succulent plants). We also expected that SOM would be higher in wetlands that receive minimal terrigenous sediment input (i.e., biogenic wetland soils that develop on carbonate platforms would have higher SOM than minerogenic soils that receive high terrigenous sediment input; Breithaupt et al., 2017; McKee et al., 2007). Since topography affects inundation, sediment supply, and salinity, which all affect plant productivity, we hypothesized that elevation would have a large influence on SOM (Hayes et al., 2017; Saintilan, Rogers, Mazumder, & Woodroffe, 2013). Finally, we expected that salinity influences would be directly tied to precipitation variations, which regulate the degree of dilution and concentration of salts.

Our research was designed to address the above-described multipart hypothesis. In addition to bivariate analyses at the regional, estuary, and transect level, we used structural equation modeling to investigate how the data relationships relate to the overall hypothesis (Grace, 2006; Grace, Anderson, Olff, & Scheiner, 2010). As a first step, we developed general and coastal wetland-specific structural equation metamodels (Figure 3) as a bridge between the general ideas of Jenny (1941) and the observable expectations for our study. The generalized metamodel (Figure 3, upper metamodel) describes the expected influences of four factors (i.e., climate, biota, topography, and parent materials) on soil formation (sensu Jenny, 1941). The coastal wetland-specific metamodel (Figure 3, lower metamodel) specifies particular variables to serve as indicators for each of these four factors as well as an additional variable (salinity) known to play a critical role in coastal wetlands. In Table 1, we describe the field and geospatial data-derived variables used to represent the various components of the structural equation modeling. Our field-based data included wetland plant and soil data collected across elevation and zonation gradients within 10 estuaries that span ecologically relevant temperature and precipitation gradients in the northern Gulf of Mexico (Figure 4).

2 | MATERIALS AND METHODS

2.1 | Study area and study design

This study was conducted along the United States' northern Gulf of Mexico coast, which is a region of the world where coastal wetlands are abundant and diverse (Gosselink, 1984; Odum, McIvor, & Smith, 1982; Tunnell & Judd, 2002; Figure 4). The northern Gulf of Mexico spans two climatic gradients that greatly influence the structure and functioning of coastal wetlands. Whereas a gradient in winter
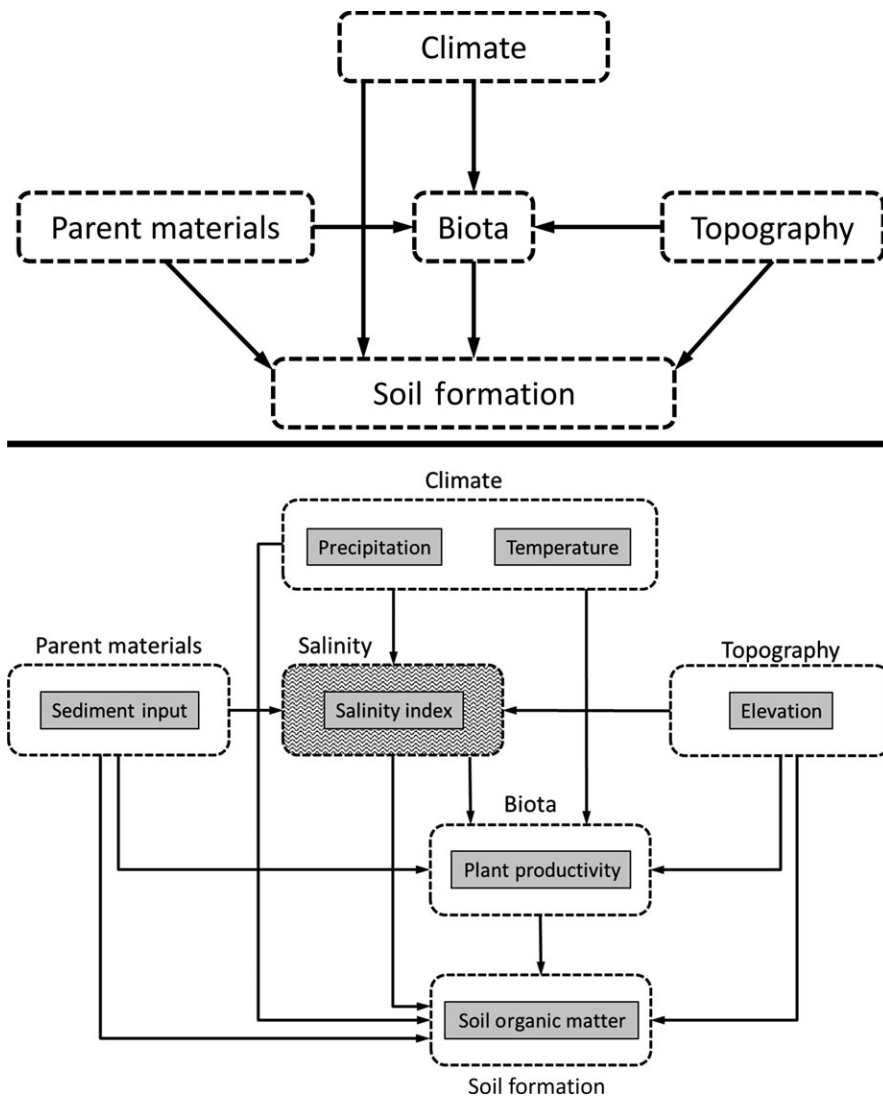
FIGURE 3 A generalized structural equation metamodel of the influence of climate, biota, topography, and parent materials upon soil formation (sensu Jenny, 1941) (upper), and our structural equation metamodel for coastal wetlands (lower). Variables are described in Table 1

TABLE 1 Description of variables used in the structural equation model and elsewhere

Factor	Variable	Source	Details	Range
Climate	Mean annual precipitation (m)	Derived from geospatial data	1981–2010; PRISM	0.7 to 1.7
Climate	Mean annual temperature (°C)	Derived from geospatial data	1981–2010; PRISM	19.6 to 23.7
Climate	Minimum temperature (°C)	Derived from geospatial data	Absolute minimum temperature; 1981–2010; PRISM	−15.2 to −4.0
Salinity	Salinity (index)	Derived from field data	Plant cover-weighted salinity score; higher score indicates higher salinity	0.1 to 1.0
Topography	Elevation (relativized)	Derived from field data	Relativized elevation; higher score indicates higher elevation	0.0 to 1.0
Parent materials	Sediment input (MS*10^{-7} m³/kg)	Ellwood et al., 2006	Sediment magnetic susceptibility, a proxy for terrigenous sediment input; higher score indicates higher sediment input	0.0 to 3.5
Biota	Plant productivity (index)	Derived from field data	Functional group- and plant height-based productivity score; higher score indicates higher productivity	0.0 to 1.0
Soil formation	Soil organic matter (%)	Derived from soil samples	Soil organic matter in samples collected to 15-cm depth beneath the soil surface	0.4 to 74.0
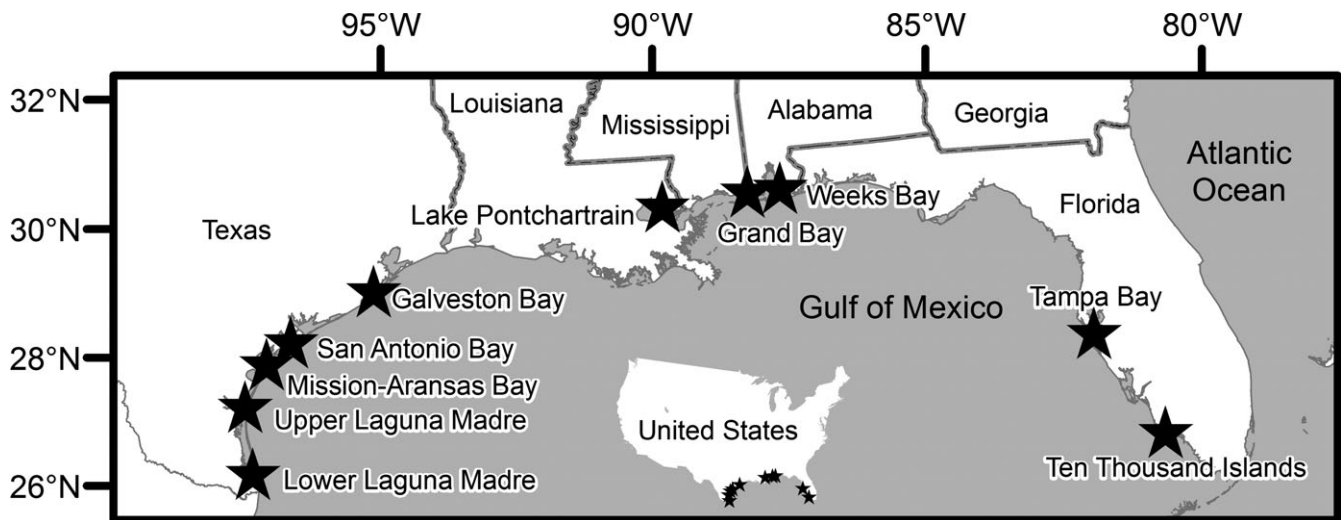
FIGURE 4 Map of the 10 northern Gulf of Mexico estuaries included in this study. The estuaries, denoted by stars, span ecologically relevant gradients in mean annual precipitation (0.7 to 1.7 m), minimum temperature (−15.2 to −4.0°C), and mean annual temperature (19.6 to 23.7°C)

temperature extremes governs the distribution of cold-sensitive mangrove forests and cold-tolerant salt marsh graminoids (Cavanaugh et al., 2014; Lugo & Patterson-Zucca, 1977; Osland et al., 2013), a gradient in precipitation governs total plant coverage, plant height, the abundance of succulent plants, and the coverage of microbial mats (Gabler et al., 2017; Longley, 1994; Osland et al., 2014). To characterize the influence of climate on the targeted ecological properties, we collected data from 10 estuaries (Figure 4; Supporting Information Figure S1), which were selected to span the region's ecologically relevant temperature and precipitation gradients. Across the study estuaries, minimum air temperature ranges from −15.2 to −4.0°C, mean annual temperature ranges from 19.6 to 23.7°C, and mean annual precipitation ranges from 0.7 to 1.7 m (Table 1; Supporting Information Figure S1). Tidal ranges in these estuaries are microtidal, ranging from approximately 0.3 to 0.6 m (Great Diurnal Range; https://tidesandcurrents.noaa.gov). Across elevation and salinity gradients within each estuary, we collected plant, soil, and elevation data from 1,020 1-m² plots. Field-based data were collected during a single visit to each plot in 2013 (September to December) or 2014 (May to December). The tidal saline wetland data were collected from 66 transects. The methods for data collection are described in more detail in Gabler et al. (2017). Here, we present results from 599 plots that were located within the tidal saline wetland zone; in other words, we excluded 421 plots that were either upslope or downslope of the tidal saline wetland zone, as described in Gabler et al. (2017).

2.2 | Plant data

Within each 1-m² plot, we measured mean plant height and species-specific plant cover for two height strata (<1.4 m and >1.4 m above the soil surface). The species-specific cover data were used to calculate coverage of the following four plant functional groups:

graminoid, mangrove, succulent, and unvegetated (i.e., no vascular plants; Gabler et al., 2017). These data were used to assign a dominant plant functional group category to each 1-m² plot. Plots with less than 25% total plant cover were considered unvegetated. If total plant cover was greater than 25%, dominance was defined by the functional group (i.e., mangrove, graminoid, or succulent) with the greatest cover. Of the 599 plots, the graminoid, mangrove, succulent, and unvegetated categories were assigned to 239, 161, 100, and 99 plots respectively. Whereas coastal wetland plant communities in the hot and wet estuaries (i.e., Tampa Bay and Ten Thousand Islands) were dominated by mangrove plant species, plant communities in the cold and wet estuaries (i.e., Weeks Bay, Grand Bay, and Lake Pontchartrain) were dominated by graminoid salt marsh species. Coastal wetlands in the drier estuaries (i.e., Lower Laguna Madre, Upper Laguna Madre, Mission-Aransas Bay, San Antonio Bay, and Galveston Bay) were either unvegetated or dominated by a mixture of succulent salt marsh, graminoid salt marsh, and mangrove plant species (Gabler et al., 2017).

We created a plant productivity index for each plot using the plant height data. Plant productivity is not always correlated to height; however, across large abiotic and plant productivity gradients like those examined in this study, coastal wetland plant height has been found to be correlated with both aboveground biomass and productivity (Alongi, 2009; Castañeda-Moya, Twilley, & Rivera-Monroy, 2013; Cintrón, Lugo, Pool, & Morris, 1978; Clough, 1992; Lugo & Snedaker, 1974; Mendelssohn & Morris, 2000; Morris & Haskin, 1990; Radabaugh, Powell, Bociu, Clark, & Moyer, 2017; Reef, Feller, & Lovelock, 2010; Rovai et al., 2016; Smith, 1992). To justify our approach for creating this index, we provide examples from the mangrove and salt marsh literature of positive relationships between plant height and productivity (Supporting Information Figure S2), using data from: (a) mangrove forests in Everglades National Park (Castañeda-Moya et al., 2011, 2013); (b) salt marshes in the USA

and Australia (Clarke & Jacoby, 1994; Dame & Kenny, 1986; Kruczynski, Subrahmanyam, & Drake, 1978; Reidenbaugh, 1983, 1983); and (c) a global review of mangrove forests (Komiyama, Ong, & Poungparn, 2008). Mangrove forests and salt marshes can both be highly productive ecosystems despite large differences in vegetation height and aboveground biomass (Feher et al., 2017); for this reason, we created an index for mangroves and a separate index for the three nonforest groups (i.e., the graminoid, succulent, and unvegetated categories) to make the data as internally consistent as possible. For plots where mangroves were dominant, we divided the mean plant height of the plot by the maximum mean plant height for all mangrove plots. For plots where the graminoid, succulent, or unvegetated functional groups were dominant, we divided the mean plant height of the plot by the maximum mean plant height for all graminoid, succulent, and unvegetated plots. Our calculations produced a plant productivity index that ranged from 0 to 1, and the conditions represented by this index range from low productivity to high productivity, respectively.

2.3 | Soil data

Within each 1-m² plot, we collected a soil sample to 15-cm depth beneath the soil surface using a custom-made, stainless steel coring device (4.7-cm diameter, split cylinder corer with a piano hinge; Osland et al., 2012). While in the field, samples were stored in a cooler with ice packs. Upon return to the laboratory, samples were stored at 4°C until processing. In the laboratory, soils were dried at 60°C to a constant mass, homogenized with a mortar and pestle, and sieved through a 2-mm screen. Samples were then further homogenized using a planetary mill (Fritsch Pulviresette, New York, NY, USA). Soil bulk density was determined as the dry weight to volume ratio (Blake & Hartge, 1986). SOM was determined via loss on ignition in a muffle furnace at 475°C for 16 hr (Karam, 1993; Wang, Li, & Wang, 2011).

2.4 | Elevation data

We measured the horizontal position and soil surface elevation relative to the North American Vertical Datum of 1988 (NAVD88) of each 1-m² plot using a high-precision Global Navigation Satellite System (GNSS; Trimble R8 and TSC3, Trimble Inc, Sunnyvale, CA, USA), in combination with real-time Continuously Operating Reference Station (CORS) networks where available (i.e., LSU's GULFNet network, Texas' TxDOT network). For each estuary, the vertical distance between the upper and lower boundaries of the tidal saline wetland zone, as defined and described in Gabler et al. (2017), was divided into four equal tidal elevation quartiles, and each plot was assigned to one of the four quartiles. Within each estuary, we also relativized the elevation data using these estuary-specific upper and lower zone boundaries.

2.5 | Climate data

Climate data were obtained for the 30-year period extending from 1981–2010. For precipitation and temperature, we obtained

continuous gridded climate data created by the PRISM Climate Group (Oregon State University; https://prism.oregonstate.edu) using the PRISM (Parameter-elevation Relationship on Independent Slopes Model) interpolation method (Daly et al., 2008). We used the horizontal coordinates and the 2.5-arcmin resolution PRISM gridded data to determine the 30-year mean annual precipitation, 30-year mean annual temperature, and the 30-year absolute minimum temperature (i.e., the coldest temperature recorded during the 30-year period) for each of our study plots. The 30-year absolute minimum temperature variable was selected due to strong positive sigmoidal relationships with the following response variables: (a) mangrove and salt marsh dominance (Gabler et al., 2017; Osland et al., 2013; Osland, Feher, et al., 2017); and (b) coastal wetland vegetation height and biomass (Feher et al., 2017; Gabler et al., 2017). In this region, growing degree days is highly correlated to 30-year mean annual temperature, and the 30-year mean annual temperature variable was selected due to a positive linear relationship with aboveground productivity (Feher et al., 2017). The 30-year mean annual precipitation variable was selected due to its positive sigmoidal relationships with the following response variables: (a) vegetation coverage in coastal wetlands (Gabler et al., 2017; Osland et al., 2014); and (b) coastal wetland vegetation height (Feher et al., 2017; Gabler et al., 2017). For more information regarding the selection of these three climatic variables, see Osland et al. (2013), Osland et al. (2014), Osland, Feher, et al., 2017, Gabler et al. (2017), and Feher et al. (2017). For more information regarding the influence of winter temperature extremes on century-scale mangrove expansion and contraction, see Osland, Day, et al., 2017.

2.6 | Salinity index

In coastal and freshwater wetlands, vegetation-based indices can be used to characterize long-term abiotic conditions (e.g., hydrology, salinity) that are too expensive or logistically difficult to measure in a large number of sites (Schweiger, Grace, Cooper, Bobowski, & Britten, 2016; Tiner, 1991; Visser, Sasser, Chabreck, & Linscombe, 1998). It would have been prohibitively challenging and costly for us to acquire long-term salinity data from each of the 599 plots. Hence, to characterize the salinity regime of each plot, we created a vegetation-based salinity index. First, we assigned a salinity tolerance score to each plant species using information contained in Visser et al. (1998), Stutzenbaker (2010), Visser, Sasser, Chabreck, and Linscombe (2002), and Lovelock, Krauss, Osland, Reef, and Ball (2016). We then used the species' salinity scores (Supporting Information Table S1) and the species-specific cover data to calculate a proxy index for plot salinity (i.e., for each plot, the species-specific cover data were multiplied by the species' salinity scores). The salinity index ranged from 0 to 1, and the conditions represented by this index range from low salinity (i.e., fresh) to high salinity (i.e., hypersaline). To justify our approach for creating this index, we show the positive relationship between a similar vegetation-based salinity index and long-term salinity measurements using vegetation and salinity data from Louisiana's Coastwide Reference and Monitoring System (Supporting Information Figure S3).

2.7 | Sediment input data

Soil organic matter concentrations are typically highest in biogenic soils that develop on carbonate platforms with very little riverine sediment input. Due to minimal allochthonous sediment and nutrient inputs, biogenic soils are composed primarily of autochthonous plant inputs, which can result in high SOM concentrations. In the Gulf of Mexico region, carbonate platforms and biogenic soils are most common along the coasts of Florida, Cuba, and the Yucatan Peninsula of Mexico. To distinguish between coastal wetlands growing on sediment-rich terrigenous substrates (i.e., minerogenic soils with high sediment input) and coastal wetlands growing on calcareous carbonate-rich substrates (i.e., biogenic soils with low sediment input), we used a Gulf of Mexico-wide sediment magnetic susceptibility dataset contained within Ellwood, Balsam, and Roberts (2006). For each of our 10 estuaries, we assigned a sediment magnetic susceptibility measurement from Ellwood et al. (2006) and used that measurement as a proxy for terrigenous sediment input. We used these data to distinguish between coastal wetlands that receive low terrigenous sediment input (i.e., magnetic susceptibility values less than or equal to 1 MS $\times$ 10^{-7} m^3/kg) versus high terrigenous sediment input (i.e., magnetic susceptibility values greater than 1 MS $\times$ 10^{-7} m^3/kg).

2.8 | Data analyses

Regression analyses, using estuary means and equations to represent the hypothesized relationships shown in Figure 2 (i.e., linear, sigmoidal, or exponential rise to maximum equations), were evaluated and used to quantify the relationships between climatic variables (i.e., mean annual precipitation and mean annual temperature) and the following dependent variables: salinity, plant productivity, and SOM. Regression analyses, using estuary means, were also used to quantify the relationships between: (a) salinity and plant productivity; and (b) plant productivity and SOM. Our data include minerogenic and biogenic wetland soils, which vary greatly in sediment input and SOM content. For SOM, we present regression analyses for three different sediment input categories: (a) all coastal wetlands; (b) coastal wetlands that receive low terrigenous sediment input; and (c) coastal wetlands that receive high terrigenous sediment input, as defined by the magnetic susceptibility data. Our data lack information from arid coastal wetlands that also receive low terrigenous sediment input. Hence, for the low terrigenous sediment input regression, we assumed that SOM in arid climates is comparatively low and similar regardless of whether the wetland is growing on a carbonate platform and receives high or low terrigenous sediment input.

We used analysis of variance to compare SOM within each of the following three plant functional group categories: salt flat without vascular plants, succulent salt marsh plants, and a combined category that included graminoid salt marsh and mangrove plants. The decision to combine the mangrove and graminoid groups was based upon: (a) the absence of consistent differences between SOM in the mangrove and graminoid salt marsh groups within an estuary (Supporting Information Figure S4); and (b) results from previous studies in Louisiana and north Florida that measured similar bulk soil properties in mangrove forests and the adjacent graminoid-dominated salt marshes (Doughty et al., 2016; Henry & Twilley, 2013; Perry & Mendelssohn, 2009; Yando et al., 2016; Yando, Osland, & Hester, 2018). Post hoc mean comparisons of these functional groups were conducted using Tukey's Studentized Range (HSD) tests.

In addition to the region-level analyses, we also conducted analyses at the estuary and transect level. For each estuary, we used Spearman rank correlations to evaluate the relationships between elevation, salinity, plant productivity, and soil organic matter. At the transect level, we used Spearman rank correlations to identify the number of transects with positive, negative, or nonsignificant relationships between elevation and the following three response variables: salinity, plant productivity, and SOM. We compared the effects of elevation within the following three transect categories: (a) transects with minimal change in salinity; (b) transects with an increase in salinity (i.e., at least a 0.25 increase in the salinity index) with elevation; and (c) transects with a decrease in salinity with elevation.

To address the overall hypothesis associated with Figure 3 (bottom subfigure), we used structural equation modeling procedures, following the guidelines presented in Grace et al. (2012). Descriptions of the variables evaluated for inclusion in the model are shown in Table 1. Mean annual temperature and minimum temperature were observed to be highly correlated in this region (R^2 = 0.83). Based upon a comparison of the effect of these two variables in initial models and after considering the primary nature of the influence of mean annual temperature on plant productivity (Feher et al., 2017), we decided to use mean annual temperature, rather than minimum temperature, to represent air temperature in the model. Estimation and evaluation were conducted using local estimation procedures to allow for more detailed model specifications. In this approach, each endogenous (response) variable constitutes a submodel within the SE model, and each was estimated separately using mixed-effect models that were specified and evaluated using the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017). Within the mixed models, estuary was treated as a random effect to account for nesting. Evaluation of parameter significance was performed using the Satterthwaite method (Fai & Cornelius, 1996). Once the three submodels (soil organic matter, plant productivity, and salinity) that make up the full structural equation model were estimated, conditional independence among submodels was tested. Data analyses were conducted in R (R Core Team, 2017) and Sigma Plot (Systat Software, San Jose, CA, USA). Spatial analyses were conducted in Esri ArcGIS (Environmental Systems Research Institute, Redlands, CA, USA).

3 | RESULTS

3.1 | Region-level relationships using estuary means

Our analyses of estuary means reveal strong linear bivariate relationships between precipitation and: (a) salinity (–); (b) plant productivity

(+); and (c) SOM (+) (Figure 5, upper, middle, and lower left panels, respectively), but no significant bivariate relationships between temperature and these same three response variables (Figure 5, right panels). In general, the drier estuaries (i.e., those in Texas, especially along the south and central Texas coast) had higher salinities, lower plant productivity, and lower SOM (Figure 5). Conversely, estuaries in Louisiana, Mississippi, Alabama, and Florida, which received higher rainfall and freshwater inputs, had lower salinities, higher plant productivity, and higher SOM (Figure 5). We suspect that the positive effect of precipitation on plant productivity was due primarily to increased productivity in the graminoid salt marsh and mangrove plant functional groups (Supporting Information Figure S5). For the relationship between precipitation and SOM, we present linear regressions for the three sediment input groups: low terrigenous sediment input, all data, and high terrigenous sediment input (Figure 5, lower left panel; dotted, solid, and short dash lines, respectively). The slopes of these three lines are: 22.9, 13.4, 5.3%/m, respectively. There was a strong linear relationship between salinity and plant productivity (−) (Figure 6, upper panel) and a strong linear relationship between plant productivity and SOM (+) (Figure 6, lower panel). For the relationship between plant productivity and SOM, we present linear regressions for the three sediment input groups (Figure 6, lower panel; dotted, solid, and dashed lines). The low terrigenous sediment input group had the highest rate of increase in SOM per increase in plant productivity or precipitation (Figures 5 and 6). SOM is often inversely correlated with soil bulk density, and in
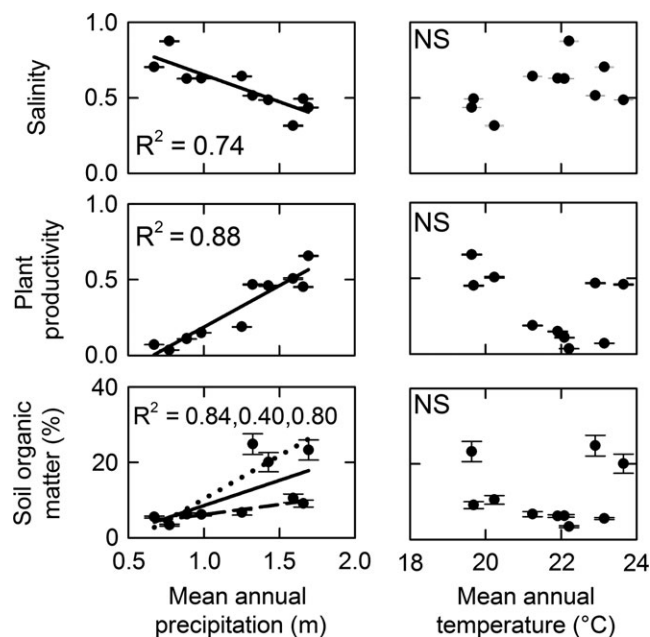
Supporting Information Figures S6 and S7, we show relationships similar to those shown in Figures 5 and 6 but with soil bulk density as the response variable rather than SOM.

As mentioned previously, there were no consistent differences in SOM between the mangrove and graminoid salt marsh groups (Supporting Information Figure S4). However, SOM in the combined mangrove and graminoid salt marsh plant group was about threefold higher than the other two plant functional groups; in other words, SOM in the combined mangrove and graminoid salt marsh plant group was higher than in: (a) the salt flat without vascular plant group; or (b) the succulent salt marsh plant group (Figure 7).

3.2 | Estuary-level relationships

Within estuaries, the relationships between elevation, salinity, plant productivity, and soil organic matter were variable. Of 60 Spearman rank correlations conducted for the relationships between these four variables within the 10 estuaries, just over half (i.e., 53%, 32

FIGURE 5 Bivariate relationships between climate and salinity (upper panels), plant productivity (middle panels), and soil organic matter (lower panels). Each point represents an estuary-level mean ± *SE*. NS = not significant. For the lower-left panel, three regression lines are shown: low terrigenous sediment input (dotted line: R^2 = 0.84), all data (solid line: R^2 = 0.40), and high terrigenous sediment input (short dash line: R^2 = 0.80)

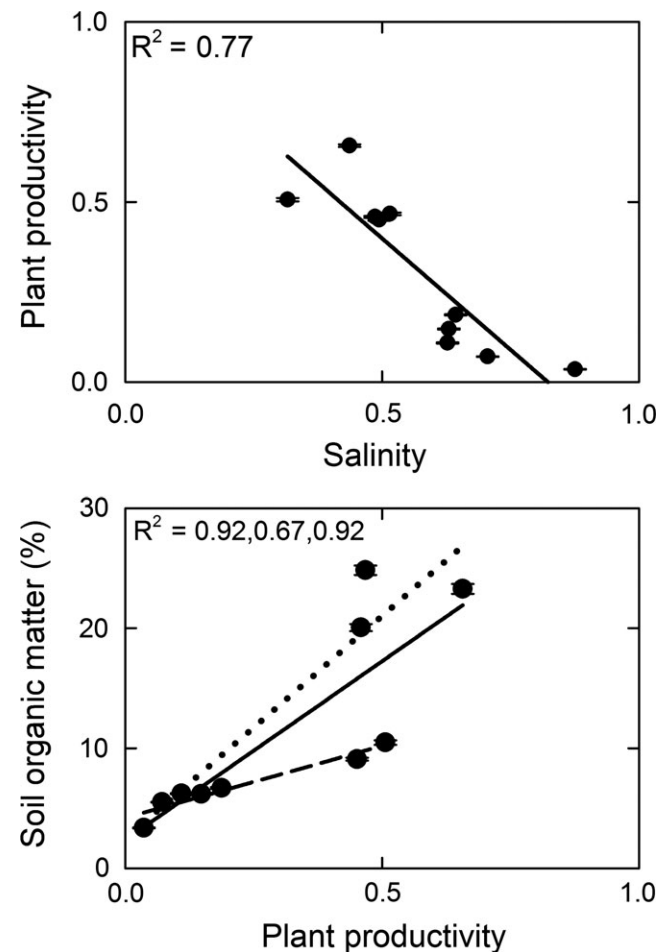**FIGURE 6** Bivariate relationships between: (upper) salinity and plant productivity; and (lower) plant productivity and soil organic matter. Each point represents an estuary-level mean ± *SE*. For the lower panel, three regression lines are shown: low terrigenous sediment input (dotted line: R^2 = 0.92), all data (solid line: R^2 = 0.67), and high terrigenous sediment input (short dash line: R^2 = 0.92)
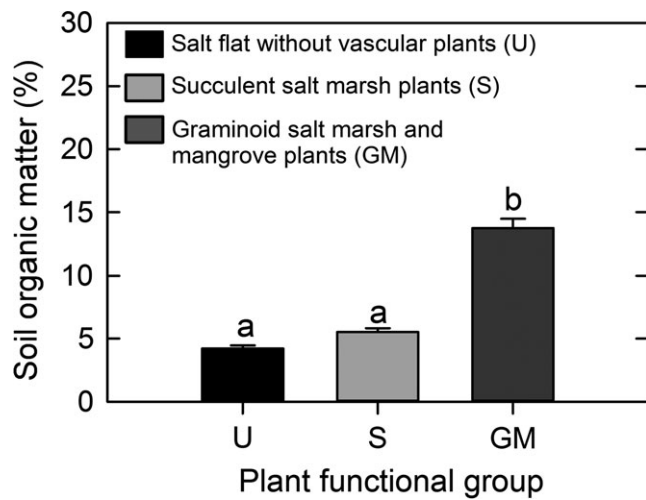
FIGURE 7 Mean ± *SE* soil organic matter within three plant functional groups. Different letters denote significant differences across categories

relationships) were significant (Supporting Information Table S2). In four of the 10 estuaries, there were positive relationships between plant productivity and SOM. In three of the 10 estuaries, there were negative relationships between salinity and SOM. In general, drier estuaries (i.e., those in Texas) had positive relationships between elevation and salinity (4 of 5 estuaries) and negative relationships between salinity and plant productivity (3 of 5 estuaries). In contrast, there were negative relationships between elevation and salinity in three of the five wetter estuaries (i.e., estuaries not in Texas).

3.3 | Transect-level relationships

At the transect level, the influence of elevation on SOM was clearly important in some areas but highly variable (Table 2; Supporting Information Table S3, Figures S8 and S9). In more than two-thirds of the transects, the relationships between elevation and salinity, plant productivity, or SOM were not significant (70%, 74%, and 73% of all transects respectively) (Table 2; Supporting Information Table S3,

Figure S9, right panels). However, in some transects, there were strong positive or negative relationships between elevation and salinity, plant productivity, and/or SOM (Table 2; Supporting Information Table S3, Figure S9, left and middle panels). For transects that were close to ground or surface freshwater inputs and where salinity decreased across the transect (e.g., some transects within the Weeks Bay [Alabama] and Lake Pontchartrain [Louisiana] estuaries), the relationships between elevation and salinity, plant productivity, and SOM had the potential to be negative, positive, and/or positive, respectively (Table 2; Supporting Information Figure S9, middle panels). However, in certain transects that spanned large elevation gradients and/or were not close to large freshwater inputs (e.g., transects in drier estuaries in Texas as well as some transects in wetter estuaries that spanned large gradients and transitioned into salt pannes at higher elevations), salinity increased across the transect and the relationships between elevation and salinity, plant productivity, and SOM had the potential to be positive, negative, and/or negative respectively (Table 2; Supporting Information Figure S9, left panels).

3.4 | Structural equation model results

Of the 15 pathways in the initial structural equation metamodel (Figure 3, lower panel), five nonsignificant pathways (as judged by significance tests using the Satterthwaite method) were excluded from the final model (Figure 8). The final model accounted for 34% of the variation in SOM, 57% for plant productivity, and 55% for salinity. Relative effect strength for individual pathways was computed based on the relevant range standardization method (Grace, Johnson, Lefcheck, & Byrnes, 2018). Note that as with all standardized partial effects, values are not constrained to fall between +1 and −1. The inference from the final model is that the variable having the greatest effect on SOM is plant productivity, which is, in turn, influenced by precipitation and salinity. Results further indicate that precipitation also affects SOM positively via an indirect pathway that passes through salinity and plant productivity (indirect effect = −1.15 × −0.23 = +0.26; Figure 8). Salinity has direct effects on plant productivity, and thus has a negative indirect effect on SOM

TABLE 2 Number of transects with positive, negative, or nonsignificant relationships between elevation and three response variables (salinity, plant productivity, and soil organic matter) within the following three transect groupings: (a) transects with minimal change in salinity; (b) transects with an increase in salinity (i.e., at least a 0.25 increase in the salinity index) with elevation; and (c) transects with a decrease in salinity with elevation. Percentages represent the percent of the total number of transects within a transect group

| Transect category	Response variable	Positive relationship	Negative relationship	Nonsignificant
Minimal change in salinity	Salinity	5 (16%)	0 (0%)	26 (84%)
	Plant productivity	3 (10%)	2 (6%)	26 (84%)
	Soil organic matter	4 (13%)	2 (6%)	25 (81%)
Salinity increase	Salinity	11 (50%)	0 (0%)	11 (50%)
	Plant productivity	0 (0%)	8 (36%)	14 (64%)
	Soil organic matter	1 (5%)	7 (32%)	14 (64%)
Salinity decrease	Salinity	0 (0%)	4 (31%)	9 (69%)
	Plant productivity	3 (23%)	1 (8%)	9 (69%)
	Soil organic matter	4 (31%)	0 (0%)	9 (69%)
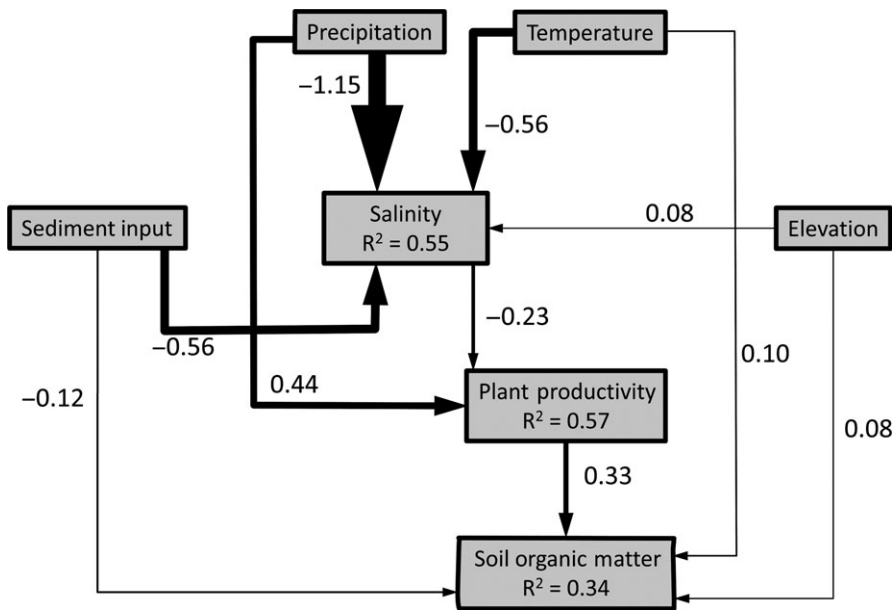
FIGURE 8 Final structural equation model of environmental controls on SOM. Path arrow thickness reflects the strength of the relationship (thicker = stronger relationship). The numbers next to the path arrows indicate the standardized effect estimates and the direction of their relationship (+ or −). The R^2 for the three endogenous variables (salinity, plant productivity, and SOM) are shown within their respective boxes. All relationships shown were statistically significant ($p < 0.05$)

($-0.23 \times 0.33 = -0.08$; Figure 8). Temperature, elevation, and sediment input also have direct and/or indirect effects on SOM in the final model; however, the total effects of precipitation via direct and indirect pathways mediated by plant productivity appear to be the more important and largest drivers of SOM variation across the study region.

4 | DISCUSSION

One of our overarching objectives was to clarify how SOM in northern Gulf of Mexico coastal wetlands is influenced by the following four soil formation factors: biota, climate, parent materials, and topography (sensu Jenny, 1941). Our analyses show that the relative influence of each of these factors is scale and location dependent. For example, at the local scale, inundation, salinity, and sediment supply greatly influence physical and biological processes, which can affect local-scale variation in SOM (Hayes et al., 2017; Kelleway, Saintilan, Macreadie, & Ralph, 2016; Saintilan et al., 2013; Stagg, Schoolmaster, Krauss, Cormier, & Conner, 2017). Hence, at transect and estuary scales, topography and biota have the potential to greatly influence SOM. However, at the regional scale, our results indicate that climate (i.e., precipitation, including its influence on salinity) and biota (i.e., plant productivity) have the potential to have a very large influence on SOM. In the subsequent paragraphs, we discuss the role of climatic and biotic controls on SOM in more detail. We also examine the importance of parent materials (i.e., sediment input) and topography (i.e., elevation). Following each subsection heading, we included the relevant soil formation factor(s) in parentheses.

4.1 | Precipitation, salinity, and plant productivity (Climate and Biota)

Across precipitation gradients that span the transition from humid to arid climates, there is often: (a) a decrease in the coverage of coastal

wetland plants (Bucher & Saenger, 1994; Gabler et al., 2017; Longley, 1995; Montagna, Gibeaut, & Tunnell, 2007; Osland et al., 2014; Osland, Feher, et al., 2017); (b) a decrease in coastal wetland plant canopy height (Feher et al., 2017; Gabler et al., 2017; Lot-Helgueras, Vázquez-Yanes, & Menéndez, 1975; Méndez-Alonzo, López-Portillo, & Rivera-Monroy, 2008); (c) a decrease in aboveground biomass (Gabler et al., 2017; Hutchison, Manica, Swetnam, Balmford, & Spalding, 2014; Rovai et al., 2016); and (d) a shift in coastal wetland plant functional group dominance, from plant communities dominated by graminoid and/or mangrove plants to plant communities dominated by succulent salt marsh plants and/or microbial mats (i.e., wetlands that lack vascular plants; unvegetated salt flats) (Gabler et al., 2017; Saenger, 2002; Yando et al., 2016).

Salinity is the abiotic factor that is often primarily responsible for these shifts in plant community composition and structure across precipitation gradients. In arid and semi-arid climates that receive little precipitation, high evaporation rates that exceed freshwater inputs can lead to hypersaline conditions as oceanic, tidally delivered salts become concentrated (Lovelock, Feller, et al., 2017; Zedler, 1982). From a physiological perspective, hypersaline conditions affect water uptake, transport, and loss; hence, plants growing in these stressful conditions must employ water acquisition strategies that are energetically costly (Ball, 1988; Nguyen et al., 2017; Reef & Lovelock, 2014). As a result, there are only a small number of vascular plant species that can tolerate the high salinities and low osmotic water potentials present in hypersaline, arid, and semiarid coastal wetlands (Ball, 1998; Clough, 1992; Lovelock et al., 2016).

Despite a growing understanding of the effects of precipitation and salinity on aboveground plant community composition, height, and coverage (Buffington, Dugger, & Thorne, 2018; Feher et al., 2017; Gabler et al., 2017; Osland, Feher, et al., 2017), the effects of precipitation and salinity on soil and belowground ecosystem properties have not been thoroughly investigated. To our knowledge, there

is only one other regional or global-scale study that has evaluated the influence of precipitation on carbon-related soil properties in coastal wetlands. Using a combination of literature-derived and field-collected data from different regions, Sanders et al. (2016) identified a positive linear relationship between precipitation and belowground carbon stocks in mangrove forests. Due to a nonlinear response of plant coverage across the precipitation gradient in our study region (Gabler et al., 2017; Osland et al., 2014) and the expectation of a similar relationship for plant productivity (Feher et al., 2017; Yando et al., 2016), we had hypothesized that there would be a positive nonlinear relationship between precipitation and SOM in the northern Gulf of Mexico (Figure 2, dashed line in left panel). However, our examinations of the data and analyses identified a strong, positive linear relationship between precipitation and SOM. Our results imply that, across the northern Gulf of Mexico precipitation gradient, there may be a 1.3% increase in SOM for every 100 mm increase in precipitation; however, our results also show that the rate of change may be affected by sediment input (Figure 5).

Our findings indicate that the effects of precipitation on SOM occur primarily through indirect pathways that involve salinity and plant productivity. Across the study region, SOM was greatest in highly-productive mangrove forests and graminoid-dominated salt marshes compared to less productive succulent-plant dominated salt marshes or salt flats without vascular plants. We isolated strong linkages between precipitation and salinity (–), between salinity and plant productivity (–), and between plant productivity and SOM (+). In other words, our results indicate that low precipitation leads to higher salinities, higher salinities lead to decreases in plant productivity, and decreases in plant productivity lead to decreases in SOM. Our structural equation modeling results indicate that there may also be strong direct effects of precipitation on plant productivity. Yet, one limitation of our study is the use of indices to represent long-term salinity and plant productivity, and there is a need for mechanistic field- and greenhouse-based studies that further elucidate the direct and indirect effects of precipitation, salinity, and plant productivity on soil carbon cycling and storage in coastal wetlands. Another limitation stems from our reliance on spatial rather than temporal variation, and our understanding would benefit from experimental and long-term studies to verify these relationships and quantify the temporal linkages between changes in precipitation, salinity, plant productivity, and SOM.

4.2 | Temperature and plant productivity (Climate and Biota)

Temperature has a large influence on coastal wetland vegetation (Lugo & Patterson-Zucca, 1977; Morrisey et al., 2010; Saenger, 2002). Across the temperature gradient that spans the transition from tropical to temperate climates, there is often: (a) a nonlinear sigmoidal decrease in the abundance of coastal wetlands dominated by mangrove forests (Cavanaugh et al., 2014; Gabler et al., 2017; Osland et al., 2013; Osland, Feher, et al., 2017); (b) a nonlinear

sigmoidal increase in the abundance of coastal wetlands dominated by graminoid plants (Gabler et al., 2017; Osland et al., 2013); (c) a nonlinear sigmoidal decrease in plant canopy height (Feher et al., 2017; Gabler et al., 2017); (d) a nonlinear sigmoidal decrease in aboveground biomass (Feher et al., 2017; Gabler et al., 2017); and (e) a linear decrease in plant productivity (Feher et al., 2017; Kirwan, Guntenspergen, & Morris, 2009).

Winter air temperature is the primary driver of the nonlinear changes in vegetation observed across the tropical-to-temperate transition zone in North America. Mangrove species are sensitive to freezing and chilling temperatures, which can reduce metabolic rates, induce membrane dysfunction, disrupt water transport, limit reproduction, reduce aboveground biomass, and lead to mortality (Kozlowski & Pallardy, 1997; Larcher, 2003; Lovelock et al., 2016; Markley, McMillan, & Thompson, 1982; Stuart, Choat, Martin, Holbrook, & Ball, 2007). The northern limit of mangrove forests is governed by the frequency and intensity of winter temperature extremes, and mangroves are replaced by graminoid-dominated salt marshes in coastal wetlands that have temperatures cold enough to cause mangrove mortality (Cavanaugh et al., 2014; Cavanaugh et al., in press; Osland et al., 2013).

One of our objectives was to quantify the influence of temperature on SOM in coastal wetlands that span the transition zone from subtropical mangrove forests to temperate salt marshes. In Figure 2, we presented two alternative hypotheses regarding the influence of temperature on SOM in this transition zone. Our primary hypothesis was that there would be no change in SOM across the temperature gradient in our study region (Figure 2, straight dashed line in right panel). We also presented a secondary hypothesis of positive nonlinear sigmoidal change in SOM that corresponds with the aboveground vegetation shift from salt marsh to mangrove forest (Figure 2, sigmoidal dashed line in right panel). Our results do not support the secondary hypothesis of nonlinear sigmoidal change but they do provide support for the hypothesis of minimal change in SOM across the temperature gradient. This result is also reinforced by: (a) two reviews of literature-derived data that found no difference in soil carbon density or accumulation rates between mangrove forests and salt marshes (Chmura et al., 2003; Feher et al., 2017); and (b) studies in Louisiana and Florida that found no difference in soil properties of mangrove forests and adjacent graminoid-dominated salt marshes (Doughty et al., 2016; Henry & Twilley, 2013; Perry & Mendelssohn, 2009; Yando et al., 2016, 2018). Mangrove forests and graminoid-dominated salt marshes can both be highly productive ecosystems with the potential for high rates of soil carbon accumulation (Chmura et al., 2003; Feher et al., 2017). In our study region, the positive linear relationship between temperature and productivity may be offset by a comparable positive linear relationship between temperature and decomposition (Feher et al., 2017; Kirwan & Blum, 2011; Mueller et al., 2018), which could explain the lack of change in SOM across the temperature gradient or between mangrove forests and graminoid-dominated salt marshes.

4.3 | Sediment input (Parent materials)

Parent materials, sediment supply, and geomorphological setting greatly influence the structure and function of coastal wetlands (Lugo & Snedaker, 1974; Rovai et al., 2018; Woodroffe et al., 2016). In our analyses, we distinguished between coastal wetlands growing on sediment-rich terrigenous substrates (i.e., minerogenic soils with high sediment input) and coastal wetlands growing on carbonate platforms (i.e., biogenic soils with low sediment input). Along the Gulf of Mexico coast, SOM is typically highest in wetlands that have developed on top of carbonate platforms (e.g., in Florida, Cuba, and the Yucatan Peninsula of Mexico). As a result of low sediment inputs, wetland soils in these karstic coastal landscapes are composed primarily of plant-derived, autochthonous materials (Breithaupt et al., 2017; McKee, 2011; Rovai et al., 2018). In contrast, coastal wetlands growing on sediment-rich terrigenous substrates (e.g., Texas, Louisiana, Mississippi, western Alabama) typically have lower SOM due to the inclusion of large mineral sediment inputs. Our analyses indicate that the relationships between precipitation, salinity, plant productivity, and SOM are likely affected by sediment input, with a higher rate of increase and higher potential maximum SOM found in biogenic wetlands that receive minimal terrigenous sediment input (Figures 5 and 6).

4.4 | Elevation (Topography)

Small changes in elevation can result in large changes in wetland ecosystem structure and function. Elevation affects inundation, salinity, sedimentation, and nutrient regimes, which govern biogeochemical processes that influence plant productivity and SOM development (Mendelssohn & Morris, 2000; Morris et al., 2002; Twilley & Day, 2012). However, the influence of elevation on SOM is complex and can be positive, negative, or neutral depending upon the influence of other factors (e.g., geomorphic setting, climate, nutrient limitation, hydrology, salinity, disturbance regimes; Feller, Whigham, McKee, & Lovelock, 2003; Hayes et al., 2017; Kelleway et al., 2016; Lovelock, Sorrell, Hancock, Hua, & Swales, 2010). In this study, the region-scale influence of elevation on SOM and other factors was not as large as we had hypothesized. However, our estuary and transect-level analyses indicate that this muted regional effect is partly due to the presence of local-scale positive, neutral, and negative effects of elevation. For example, at the estuary scale, the effect of elevation on salinity was often positive in drier estuaries but had the potential to be negative in wetter estuaries. For transects where salinity decreased across the transect due to the role of large freshwater inputs, there was the potential for strong relationships between elevation and salinity (–), plant productivity (+), and SOM (+). However, in transects where salinity increased across the transect due to lack of freshwater inputs, there was the potential for strong relationships with elevation in the opposite direction (i.e., salinity [+], plant productivity [–], and SOM [–]). These contrasting results illustrate that the influence of elevation on SOM is clearly important, highly variable, and scale and location dependent.

4.5 | Climate change implications

Mangrove expansion is a phenomenon that has been observed across the world in response to many different aspects of global change. In the last two decades, there has been increasing interest in the ecological implications of climate change-induced mangrove expansion into salt marsh (Kelleway et al., 2017; Osland et al., 2016a; Perry & Mendelssohn, 2009; Saintilan et al., 2014). Future climate projections for eastern North America include warmer winter temperature extremes (Vose, Easterling, Kunkel, LeGrande, & Wehner, 2017), which is expected to result in mangrove northward expansion at the expense of salt marsh in parts of Texas, Louisiana, and Florida (Cavanaugh et al., 2014; Gabler et al., 2017; Osland et al., 2013). In general, mangrove expansion results in large increases in aboveground biomass and carbon stocks, which are changes that would have large effects on certain ecosystem services, including avian habitat, fisheries, protection of coastal communities from storms, and human recreational opportunities; however, the effects of mangrove expansion on soil carbon stocks and soil properties are diverse and context dependent. A portion of these differences may be attributed to differences in the salt marsh that is being replaced.

Our comparisons of SOM in different plant functional groups provide support for considering the role of plant productivity and plant functional group when assessing the ecological implications of mangrove expansion. As in terrestrial ecosystems (Eldridge et al., 2011; Jobbágy & Jackson, 2000), plants are important drivers of SOM development and accumulation in coastal wetlands. Our analyses identify strong relationships between plant productivity and SOM. SOM was lowest in coastal wetlands that lacked vascular plants and in coastal wetlands that were dominated by succulent salt marsh plants. In contrast, SOM was highest in wetlands dominated by productive graminoid salt marsh and mangrove plants. There was a strong relationship between SOM and the productivity of graminoid salt marsh and mangrove plants. These results suggest that in wetter portions of the northern Gulf of Mexico (e.g., Louisiana and Florida), the belowground implications of mangrove expansion into the existing graminoid-dominated salt marshes may not be as high as in drier estuaries (e.g., south Texas) where mangrove expansion may occur at the expense of salt marshes dominated by succulent plants (Yando et al., 2016, 2018). Despite these differences in the belowground implications of mangrove expansion, the aboveground implications of mangrove expansion are expected to be large across the entire region (i.e., in Texas, Louisiana, and Florida).

In addition to changing winter temperature regimes, future climate projections for the northern Gulf of Mexico indicate that the frequency and intensity of precipitation extremes are expected to increase; in other words, more frequent and intense flooding and drought are expected (Easterling, Kunkel, & Arnold, 2017). Previous studies have shown that changes in precipitation are expected to alter salinity regimes, modify the abundance and coverage of vegetation, and change the functional group composition of

coastal wetland plant communities (Diop, Soumare, Diallo, & Guisse, 1997; Dunton et al., 2001; Eslami-Andargoli et al., 2009; Gabler et al., 2017; Osland et al., 2014). Our results imply that changes in precipitation and salinity could also affect plant productivity and SOM. Whereas increases in precipitation are expected to result in lower salinity, higher plant productivity, and higher SOM, decreases in precipitation are expected to result in the converse (i.e., higher salinity, lower productivity, and lower SOM). There is a need to investigate the mechanisms that may be responsible for these expected changes as well the effects of these changes on wetland stability and the supply of ecosystem goods and services.

Drought is an aspect of climate change that merits more attention from coastal wetland scientists. Given the expectation of future increases in drought frequency and intensity, there is a pressing need to advance understanding of the effects of drought on salt marshes, mangrove forests, and salt flats. In the southeastern USA, previous droughts, in combination with trophic interactions, have contributed to acute marsh diebacks know as brown marsh events (McKee et al., 2004; Silliman, Koppel, Bertness, Stanton, & Mendelssohn, 2005). In Australia, drought, in combination with elevated temperature and lowered sea levels, contributed to large mangrove die-offs in 2015–2016 (Duke et al., 2017; Lovelock, Feller, et al., 2017). Drought has also been linked to mangrove die-off events in Senegal (Diop et al., 1997), shifts in marsh plant community composition in the northwestern Gulf of Mexico (Dunton et al., 2001), declines in marsh belowground production in the northern Gulf of Mexico (Stagg, Schoolmaster, Piazza, et al., 2017), and shifts in marsh biomass in the northwestern USA (Buffington et al., 2018). In tropical regions that have a long dry season (i.e., a tropical wet and dry climate), changes in the timing, intensity, and duration of the dry season can have large effects on wetland ecosystem structure and function (Barr et al., 2010; Fosberg, 1961; Malone, Starr, Staudhammer, & Ryan, 2013; Osland, González, & Richardson, 2011). In addition to a need to advance our knowledge of the effects of drought on salinity and plant productivity, our results indicate that there is a need to advance understanding of the effects of drought on soil organic matter, soil-surface elevation change, carbon storage, carbon cycling, and peat collapse. Peat collapse, which can occur in response to rapid vegetation die-off events (Cahoon et al., 2003), is a serious concern in coastal wetlands due to: (a) the large amount of carbon that can be released from the system (Lane et al., 2016; Lovelock, Ruess, & Feller, 2011); and (b) the large changes in surface elevation that decrease wetland stability and hinder the potential for ecosystem recovery or restoration (Baustian, Mendelssohn, & Hester, 2012). What are the potential conditions and mechanisms that would lead to drought-induced peat collapse in coastal wetlands? Due to the potential impact on wetland stability and wetland ecosystem services, the potential for drought-induced peat collapse deserves more attention (McKee et al., 2004). Our results indicate that the effects of changes in precipitation and salinity are likely modulated by sediment input. In other words, ecological responses to changes in precipitation and salinity in biogenic wetlands growing on carbonate platforms are expected to be different than in minerogenic wetlands. However, research in arid minerogenic and biogenic wetlands is scant, and there is a need for research that elucidates the mechanisms and conditions that lead to peat formation or degradation in these hypersaline ecosystems. In many estuaries, the effects of drought could be amplified by increases in upstream human water use, which often result in saltwater intrusion and reduced freshwater inputs to downstream coastal wetlands (Alber, 2002; Howard et al., 2017; Longley, 1994; Montagna, Palmer, & Pollack, 2013). Hence, there is also a need to consider the simultaneous and interactive effects of future changes in land use and anthropogenic management of the rivers that deliver water to estuaries.

Accelerated sea-level rise and saltwater intrusion are two aspects of climate change that will have a tremendous impact on coastal wetland ecosystems across the world (Conner, Doyle, & Krauss, 2007; Doyle, Krauss, Conner, & From, 2010; Kirwan & Megonigal, 2013; Scavia et al., 2002; Thorne, MacDonald, & Guntenspergen, 2018), and many of the effects of changes in temperature or rainfall will be modulated by these two drivers. For example, in arid, hypersaline estuaries, rising sea levels would be expected to push elevation-controlled salinity gradients upslope. As a result, salinities in some hypersaline wetlands may decrease due to more frequent inundation by euhaline waters; however, the salinities of higher-elevation uplands would be expected to increase and result in a transition from coastal upland vegetation to hypersaline salt flats or succulent-dominated marshes.

4.6 | Blue carbon implications

Coastal wetland scientists across the world have been working to better quantify the carbon pools and fluxes present in coastal wetlands. The term "blue carbon" has been designated to describe and communicate the importance of the large carbon stocks and high belowground carbon-sequestration rates present in mangrove forests, salt marshes, and seagrass ecosystems (Howard et al., 2014; Mcleod et al., 2011). In the last decade, an increasing number of above- and below-ground carbon inventories have been conducted for salt marshes, mangrove forests, and tidal freshwater forests at global, national, regional, and local scales (Hamilton & Friess, 2018; Hinson et al., 2017; Krauss et al., 2018; Macreadie et al., 2017; Owers, Rogers, & Woodroffe, 2018; Sanderman et al., 2018). Our precipitation-focused results highlight the importance of considering precipitation, salinity, and plant productivity as drivers of blue carbon variation (Etemadi, Smoak, & Sanders, 2018; Sanders et al., 2016; Schile et al., 2017). Our parent-material focused results reinforce the importance of distinguishing between coastal wetlands growing on sediment-rich terrigenous substrates (i.e., minerogenic soils with high sediment input) and coastal wetlands growing on calcareous carbonate-rich substrates (i.e., biogenic soils with low sediment input; Rovai et al., 2018).
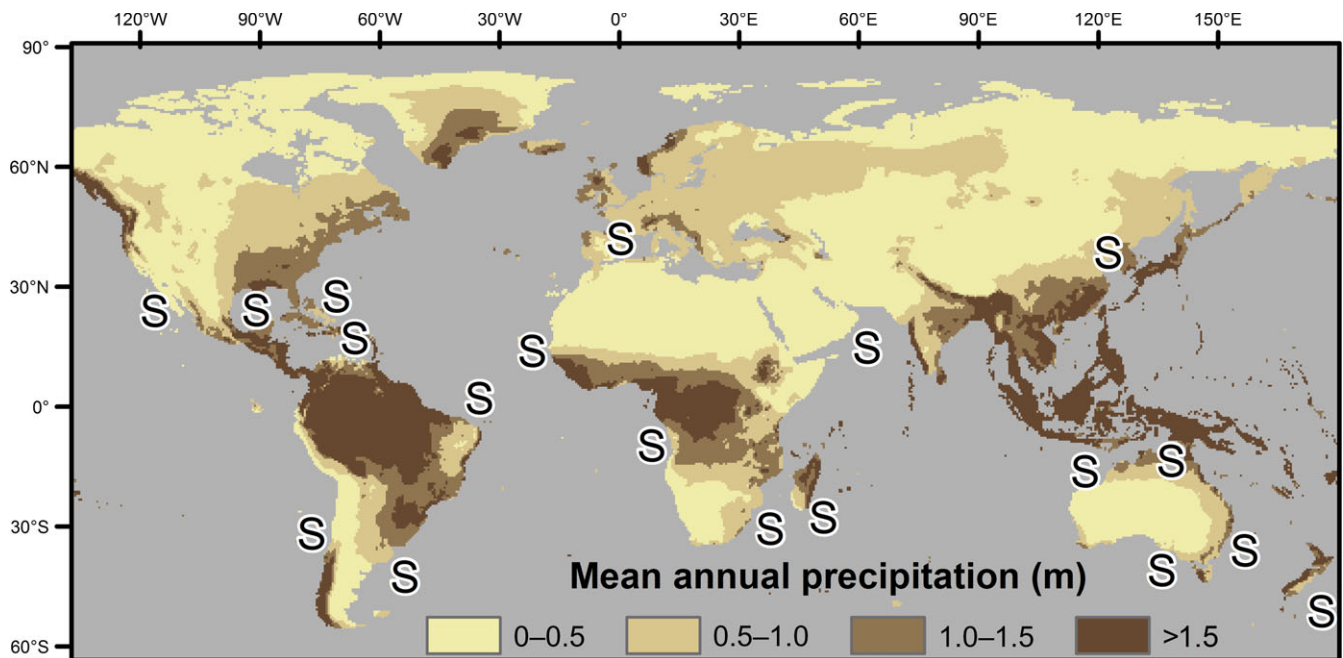
FIGURE 9 Areas where coastal wetlands are expected to be especially sensitive to changes in precipitation and freshwater availability (identified with the S symbol). In these areas, future changes in SOM and plant productivity, regulated by cascading effects of precipitation on freshwater availability and salinity, could impact wetland stability and affect the supply of some wetland ecosystem services. Precipitation data are from Hijmans, Cameron, Parra, Jones, and Jarvis (2005)

4.7 | Beyond the Gulf of Mexico: the global significance of our results

Our analyses use data from the Gulf of Mexico, but our results can be related to coastal wetlands across the globe. Our findings provide a foundation for predicting the ecological effects of future reductions in precipitation and freshwater availability. Our precipitation- and salinity-driven results are especially relevant for coastal wetlands located along coasts that currently receive low rainfall. In addition to the western Gulf of Mexico, coastal wetlands located within and near arid and semi-arid climates in the following areas are likely to be highly sensitive to changes in precipitation and freshwater availability: (a) western North America, (b) western South America, (c) Caribbean; (d) central Brazil; (e) southeastern South America; (f) Europe; (g) northwestern Africa; (h) southwestern Africa; (i) southeastern Africa; (j) Madagascar; (k) northeastern Africa; (l) Middle East; (m) eastern India; (n) northeastern Asia; (o) western Australia; (p) northern Australia; (q) eastern Australia; (r) southern Australia; and (s) New Zealand (Figure 9). These are climate-sensitive areas where there is a need for ecologists to advance understanding of climate and land use change effects on coastal wetland ecosystems.

Collectively, our results indicate that the most important drivers of regional wetland SOM variation in the northern Gulf of Mexico are precipitation, salinity, and plant productivity. Topographic variation in elevation plays a very important but variable role across the region, and sediment input appears to modulate the effects of precipitation on SOM. Precipitation in this region appears to have a greater effect on SOM than temperature. The effects of precipitation on SOM, however, appear to be indirect. SOM was greatest in

mangrove forests and in salt marshes dominated by graminoid plants. SOM was lower in salt flats that lacked vascular plants and in salt marshes dominated by succulent plants. Low precipitation leads to higher salinity, which limits plant productivity and appears to constrain SOM accumulation. Conversely, our results indicate that high precipitation decreases salinity, increases plant productivity, and increases SOM. Our analyses provide a foundation for future investigation, and there is a need for studies that evaluate the mechanisms that may be responsible for the identified relationships between precipitation, salinity, productivity, and SOM. There is also a need to test our findings across prominent precipitation gradients in other parts of the world (e.g., western North America, eastern and western South America, Europe, China, western and eastern Africa, Australia) (Figure 9). Within the context of climate change, our results indicate that changes in SOM and plant productivity, due to changes in precipitation, freshwater availability, and salinity, could impact wetland stability and affect the future supply of some wetland ecosystem services.

or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Data from this project are available via Osland et al. (2016b).

ORCID

Michael J. Osland http://orcid.org/0000-0001-9902-8692
Christopher A. Gabler http://orcid.org/0000-0001-9311-7248
James B. Grace http://orcid.org/0000-0001-6374-4726
Richard H. Day http://orcid.org/0000-0002-5959-7054
Meagan L. McCoy https://orcid.org/0000-0003-2759-3793
Jennie L. McLeod http://orcid.org/0000-0002-2998-7449
Andrew S. From http://orcid.org/0000-0002-6543-2627
Nicholas M. Enwright http://orcid.org/0000-0002-7887-3261
Laura C. Feher http://orcid.org/0000-0002-5983-6190
Camille L. Stagg http://orcid.org/0000-0002-1125-7253
Stephen B. Hartley http://orcid.org/0000-0003-1380-2769

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