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Laura Feher

*United States Geological Survey*

Michael Osland

*United States Geological Survey*

Kereen Griffith

*United States Geological Survey*

James Grace

*United States Geological Survey*

Rebecca Howard

*United States Geological Survey*

*See next page for additional authors*

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# Linear and nonlinear effects of temperature and precipitation on ecosystem properties in tidal saline wetlands

## Abstract

Climate greatly influences the structure and functioning of tidal saline wetland ecosystems. However, there is a need to better quantify the effects of climatic drivers on ecosystem properties, particularly near climate-sensitive ecological transition zones. Here, we used climate- and literature-derived ecological data from tidal saline wetlands to test hypotheses regarding the influence of climatic drivers (i.e., temperature and precipitation regimes) on the following six ecosystem properties: canopy height, biomass, productivity, decomposition, soil carbon density, and soil carbon accumulation. Our analyses quantify and elucidate linear and nonlinear effects of climatic drivers. We quantified positive linear relationships between temperature and above-ground productivity and strong positive nonlinear (sigmoidal) relationships between (1) temperature and above-ground biomass and canopy height and (2) precipitation and canopy height. Near temperature-controlled mangrove range limits, small changes in temperature are expected to trigger comparatively large changes in biomass and canopy height, as mangrove forests grow, expand, and, in some cases, replace salt marshes. However, within these same transition zones, temperature-induced changes in productivity are expected to be comparatively small. Interestingly, despite the significant above-ground height, biomass, and productivity relationships across the tropical-temperate mangrove-marsh transition zone, the relationships between temperature and soil carbon density or soil carbon accumulation were not significant. Our literature review identifies several ecosystem properties and many regions of the world for which there are insufficient data to fully evaluate the influence of climatic drivers, and the identified data gaps can be used by scientists to guide future research. Our analyses indicate that near precipitation-controlled transition zones, small changes in precipitation are expected to trigger comparatively large changes in canopy height. However, there are scant data to evaluate the influence of precipitation on other ecosystem properties. There is a need for more decomposition data across climatic gradients, and to advance understanding of the influence of changes in precipitation and freshwater availability, additional ecological data are needed from tidal saline wetlands in arid climates. Collectively, our results can help scientists and managers better anticipate the linear and nonlinear ecological consequences of climate change for coastal wetlands.

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## Authors

Laura Feher, Michael Osland, Kereen Griffith, James Grace, Rebecca Howard, Camille Stagg, Nicholas Enwright, Ken W. Krauss, Christopher Gabler, Richard Day, and Kerrylee Rogers

# Linear and nonlinear effects of temperature and precipitation on ecosystem properties in tidal saline wetlands

LAURA C. FEHER,<sup>1,†</sup> MICHAEL J. OSLAND,<sup>1</sup> KEREEN T. GRIFFITH,<sup>2</sup> JAMES B. GRACE,<sup>1</sup> REBECCA J. HOWARD,<sup>1</sup>  
CAMILLE L. STAGG,<sup>1</sup> NICHOLAS M. ENWRIGHT,<sup>1</sup> KEN W. KRAUSS,<sup>1</sup> CHRISTOPHER A. GABLER,<sup>3</sup>  
RICHARD H. DAY,<sup>1</sup> AND KERRYLEE ROGERS<sup>4</sup>

<sup>1</sup>U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, Louisiana 70506 USA

<sup>2</sup>Griffith Consulting Services at U.S. Geological Survey, Lafayette, Louisiana 70506 USA

<sup>3</sup>School of Earth, Environmental, and Marine Sciences, University of Texas Rio Grande Valley, Brownsville, Texas 78520 USA

<sup>4</sup>School of Earth and Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522 Australia

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**Abstract.** Climate greatly influences the structure and functioning of tidal saline wetland ecosystems. However, there is a need to better quantify the effects of climatic drivers on ecosystem properties, particularly near climate-sensitive ecological transition zones. Here, we used climate- and literature-derived ecological data from tidal saline wetlands to test hypotheses regarding the influence of climatic drivers (i.e., temperature and precipitation regimes) on the following six ecosystem properties: canopy height, biomass, productivity, decomposition, soil carbon density, and soil carbon accumulation. Our analyses quantify and elucidate linear and nonlinear effects of climatic drivers. We quantified positive linear relationships between temperature and above-ground productivity and strong positive nonlinear (sigmoidal) relationships between (1) temperature and above-ground biomass and canopy height and (2) precipitation and canopy height. Near temperature-controlled mangrove range limits, small changes in temperature are expected to trigger comparatively large changes in biomass and canopy height, as mangrove forests grow, expand, and, in some cases, replace salt marshes. However, within these same transition zones, temperature-induced changes in productivity are expected to be comparatively small. Interestingly, despite the significant above-ground height, biomass, and productivity relationships across the tropical–temperate mangrove–marsh transition zone, the relationships between temperature and soil carbon density or soil carbon accumulation were not significant. Our literature review identifies several ecosystem properties and many regions of the world for which there are insufficient data to fully evaluate the influence of climatic drivers, and the identified data gaps can be used by scientists to guide future research. Our analyses indicate that near precipitation-controlled transition zones, small changes in precipitation are expected to trigger comparatively large changes in canopy height. However, there are scant data to evaluate the influence of precipitation on other ecosystem properties. There is a need for more decomposition data across climatic gradients, and to advance understanding of the influence of changes in precipitation and freshwater availability, additional ecological data are needed from tidal saline wetlands in arid climates. Collectively, our results can help scientists and managers better anticipate the linear and nonlinear ecological consequences of climate change for coastal wetlands.

**Key words:** biomass; canopy height; climate change; coastal wetland; mangrove forest; nonlinear; precipitation; productivity; salt marsh; soil carbon; temperature; threshold.

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† **E-mail:** lfeher@usgs.gov

## INTRODUCTION

Across the globe, climatic drivers (i.e., temperature and precipitation regimes) greatly influence the structure and functioning of ecosystems (Jenny 1941, Holdridge 1967, Whittaker 1970, Woodward 1987, Jobbágy and Jackson 2000, Chapin et al. 2011). Within the context of climate change, understanding the ecological influence of climatic drivers is important, because it provides a foundation for anticipating and preparing for the effects of future change (Glick et al. 2011). Knowledge of ecological thresholds, nonlinear relationships, and climate-sensitive ecosystem properties can be particularly useful for predicting where and when small changes in temperature or precipitation regimes may trigger comparatively large and abrupt changes in ecosystem structure and function (i.e., regime shifts *sensu* Scheffer et al. 2001). Here, we used a combination of climate- and literature-derived ecological data to investigate the influence of temperature and precipitation regimes upon ecosystem structure and function in tidal saline wetlands.

Mangrove forests, salt marshes, and tidal salt flats are all tidal saline wetland ecosystems. Despite vegetation differences, all three of these ecosystem types occupy similar hydrogeomorphic positions within the landscape (i.e., sheltered tidally inundated saline wetland habitats). In addition to providing fish and wildlife habitat, these highly productive ecosystems improve water quality, protect coastlines, store carbon, and provide recreational opportunities (Barbier et al. 2011). Hence, the conservation and maintenance of these systems in the face of climate change are a high priority for coastal environmental managers (Alongi 2008, McKee et al. 2012, Kirwan and Megonigal 2013).

Climatic drivers govern the distribution and abundance of mangrove forests, salt marshes, and salt flats (Davis 1940, West 1977, Twilley 1982, Semeniuk 1983, Woodroffe and Grindrod 1991, Saenger 2002). Mangroves are woody plants that are sensitive to freezing and chilling temperatures; hence, mangrove forests are most common in the tropics and subtropics (Tomlinson 1986, Ross et al. 2001, Stuart et al. 2007). In contrast, salt marshes are freeze tolerant and most common in temperate, sub-arctic, and arctic climes (Pennings and Bertness 2001, Ibáñez et al. 2012). Salt flats are

hypersaline ecosystems that lack vascular plants and are most abundant along arid and semi-arid coasts (Zedler 1983, Adam 1990, Semeniuk 2013).

Climate-focused research on tidal saline wetlands has historically treated mangrove forests, salt marshes, and salt flats as different systems that occur independently. Mangrove ecologists have often examined climatic controls on ecosystem structure and function solely within mangrove forests, salt marsh ecologists have typically focused solely on salt marshes, and very little work has been conducted in salt flats partly due to lack of data (Table 1). Within a given estuary, local abiotic and biotic factors (e.g., hydrology, geomorphology, salinity, competition, facilitation) greatly influence the distribution and abundance of salt marshes, mangrove forests, and salt flats (Lugo and Snedaker 1974, Pennings and Callaway 1992, Roy et al. 2001, Krauss et al. 2008, Friess et al. 2012, Jones et al. 2016b, Gabler et al. 2017, Hayes et al. 2017); however, climatic factors greatly influence those local abiotic and biotic conditions. Hence, at the global scale, climatic factors affect the relative distribution and abundance of these different kinds of tidal saline wetland ecosystems. Several studies have used regional- or global-scale remotely sensed mangrove, salt marsh, and/or salt flat data to examine the influence of climate on plant functional group abundance (Deegan et al. 1986, Bucher and Saenger 1994, Longley 1994, Montagna et al. 2011, Osland et al. 2013, 2014b, 2017a, Cavanaugh et al. 2014, 2015, Giri and Long 2016, Rodriguez et al. 2016). However, to our knowledge, the work of Chmura et al. (2003), Gabler et al. (2017), Ouyang et al. (2017), and Simpson et al. (2017) are the only regional- or global-scale studies that have used field-based data from both mangrove forests and salt marshes to evaluate the influence of climatic drivers on a particular coastal wetland ecosystem property. These studies show that there is much to gain from examining climatic controls on these tidal saline wetland ecosystems together, as they occupy the same broad hydrogeomorphic niche (i.e., the tidal saline wetland niche) across wide regional climatic gradients; studies that just examine one system (e.g., mangrove forest or salt marsh) only examine a portion of the tidal saline wetland niche. Ecological regime shifts and oscillations are common in tidal saline wetlands, and

Table 1. Literature used to develop and test hypotheses regarding the effects of climatic drivers on ecosystem properties in tidal saline wetlands.

Property	Literature sources <sup>†‡</sup>
Canopy height	Lot-Helgueras et al. (1975) <sup>m,3</sup> , Anderson and Treshow (1980) <sup>s,1</sup> , Saenger and Snedaker (1993) <sup>m,4</sup> , Morrisey et al. (2007) <sup>m,2</sup> , Komiyama et al. (2008) <sup>m,4</sup> , Méndez-Alonzo et al. (2008) <sup>m,3</sup> , McCall and Pennings (2012) <sup>s,1,3</sup> , Soares et al. (2012) <sup>m,4</sup> , Lovelock et al. (2016) <sup>m,4</sup> , Rovai et al. (2016) <sup>m,1,3</sup> , Yando et al. (2016) <sup>s,m,3</sup> , Gabler et al. (2017) <sup>s,m,3</sup> , Guo et al. (2017) <sup>s,m,3</sup> , Simpson et al. (2017) <sup>s,m,1</sup>
Above-ground biomass	Turner (1976) <sup>s,1</sup> , Twilley et al. (1992) <sup>m,4</sup> , Saenger and Snedaker (1993) <sup>m,4</sup> , Bucher and Saenger (1994) <sup>m,2</sup> , Saenger (2002) <sup>m,1,2</sup> , Morrisey et al. (2007, 2010) <sup>m,2</sup> , Komiyama et al. (2008) <sup>m,4</sup> , Alongi (2009) <sup>m,4</sup> , Kirwan et al. (2009) <sup>s,1</sup> , Twilley and Day (2012) <sup>m,4</sup> , Asbridge et al. (2015) <sup>m,2</sup> , Lovelock et al. (2016) <sup>m,4</sup> , Rovai et al. (2016) <sup>m,1,3</sup> , Sanders et al. (2016) <sup>m,2</sup> , Yando et al. (2016) <sup>s,m,3</sup> , Gabler et al. (2017) <sup>s,m,3</sup> , Schile et al. (2017) <sup>s,m,4</sup>
Above-ground primary productivity	Turner (1976) <sup>s,1</sup> , Twilley et al. (1992) <sup>m,4</sup> , Saenger and Snedaker (1993) <sup>m,4</sup> , Saenger (2002) <sup>m,1,2</sup> , Komiyama et al. (2008) <sup>m,4</sup> , Alongi (2009) <sup>m,4</sup> , González Trilla et al. (2009) <sup>s,4</sup> , Kirwan et al. (2009) <sup>s,1</sup> , Morrisey et al. (2007, 2010) <sup>m,2</sup> , Twilley and Day (2012) <sup>m,4</sup> , Day et al. (2013) <sup>s,1</sup> , Osland et al. (2014a, b) <sup>s,m,3</sup> , Asbridge et al. (2015) <sup>m,2</sup> , Lovelock et al. (2016) <sup>m,4</sup>
Decomposition	Kirwan and Blum (2011) <sup>s,1</sup> , Kirwan et al. (2014) <sup>s,1</sup> , Crosby et al. (2017) <sup>s,1</sup> , Ouyang et al. (2017) <sup>s,m,1</sup>
Soil carbon density and accumulation	Chmura et al. (2003) <sup>s,m,4</sup> , Craft (2007) <sup>s,1</sup> , Kristensen et al. (2008) <sup>m,4</sup> , Perry and Mendelsohn (2009) <sup>s,m,3</sup> , Comeaux et al. (2012) <sup>s,m,3</sup> , Bianchi et al. (2013) <sup>s,m,3</sup> , Henry and Twilley (2013) <sup>s,m,3</sup> , Jardine and Siikamäki (2014) <sup>m,4</sup> , Ouyang and Lee (2014) <sup>s,4</sup> , Doughty et al. (2016) <sup>m,1</sup> , Kelleway et al. (2016) <sup>s,m,2</sup> , Sanders et al. (2016) <sup>m,2</sup> , Yando et al. (2016) <sup>s,m,3</sup> , Guo et al. (2017) <sup>s,m,3</sup> , Schile et al. (2017) <sup>s,m,4</sup>

<sup>†</sup> Habitat: s, salt marsh; m, mangrove.

<sup>‡</sup> Transition zone: 1, eastern North America; 2, eastern Australia; 3, western Gulf of Mexico; 4, global.

the identification of global- and regional-scale ecological thresholds, transition zones, and climate–ecological linkages can be achieved via holistic analyses that span the entire tidal saline wetland niche and include ecological data from mangrove forests, salt marshes, and salt flats (Osland et al. 2016, Gabler et al. 2017).

In this study, our overarching aim was to quantify the influence of temperature and precipitation regimes upon the following six ecosystem properties in tidal saline wetlands: canopy height, above-ground biomass, above-ground productivity, decomposition, soil carbon density, and soil carbon accumulation. These properties greatly influence the many ecosystem goods and services that wetlands provide including storm protection, erosion prevention, nutrient cycling, trophic linkages, fish and wildlife habitat, and carbon storage (Barbier et al. 2011, Kelleway et al. 2017). Due in part to high productivity and anaerobic conditions that limit decomposition, tidal saline wetlands have the potential for high rates of soil carbon storage; soil carbon stocks and carbon accumulation rates in tidal saline wetlands are often higher than their terrestrial counterparts (Chmura et al. 2003, Donato et al. 2011, McLeod et al. 2011, Atwood et al. 2017, Macreadie et al. 2017). Hence, carbon cycling and storage have been widely studied and emphasized in the tidal

saline wetland literature, and data for the six selected ecosystem properties are available and consolidated in reviews (Table 1). Our objectives were to use literature-derived data from all tidal saline wetland types to determine the influence of climatic drivers (i.e., temperature and precipitation) on the selected ecosystem properties. Based upon a review of the coastal wetland and terrestrial ecological literature (Table 1), we developed hypotheses regarding the influence of temperature and precipitation upon each of the six targeted ecosystem properties (Fig. 1). Given space constraints in this introduction, our description of and rationale for each of the selected hypotheses is explained in detail in tandem with the results in the discussion section of this manuscript. For each of the hypothesized relationships, we sought regional-scale literature-derived ecological data that could be used to quantify climate–ecological linkages. These literature-derived data were obtained from prior reviews as well as individual studies that examined global patterns of ecosystem structure and function in tidal saline wetlands (Table 1). Note that most of these reviews focus on salt marshes or mangrove forests separately (see symbols in Table 1), and Chmura et al. (2003) and Ouyang et al. (2017) are the only two reviews that have incorporated data from both mangrove forests and salt marshes. We

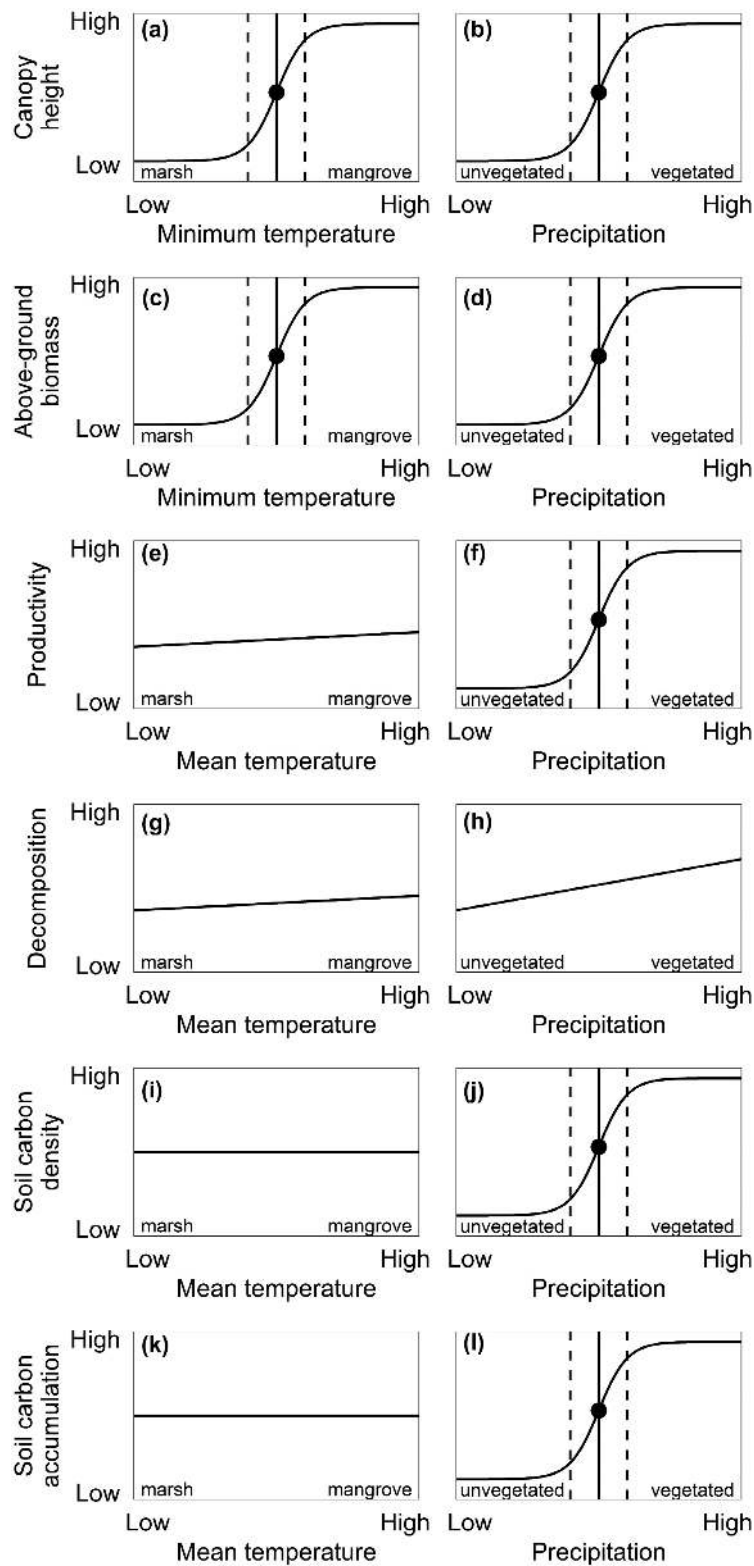


Fig. 1. Hypothesized relationships between climatic drivers and ecological properties of tidal saline wetlands:



(Fig. 1. *Continued*)

vegetation canopy height (a, b), above-ground biomass (c, d), above-ground productivity (e, f), decomposition (g, h), soil carbon density (i, j), and soil carbon accumulation (k, l). For sigmoidal relationships, the inflection point (black dot) represents a discrete threshold and the dashed lines represent a threshold zone. The rationale for these hypotheses is provided in the discussion section.

used our climate- and literature-derived data to address the following questions: (1) “What is the influence of temperature and precipitation on canopy height, above-ground biomass, above-ground primary productivity, decomposition, soil carbon density, and soil carbon accumulation in tidal saline wetlands?” (2) “Are there nonlinear relationships and temperature- and precipitation-based thresholds for these six ecological properties?” (3) “How do the identified climate–ecological relationships for tidal saline wetlands compare to those from terrestrial ecosystems?” and (4) “What data limitations affect our understanding of the influence of climatic drivers and climate change on ecosystem structure and function in tidal saline wetlands?”

## METHODS

### *Study area*

Our study area initially encompassed the entire globe, and we attempted to obtain literature-derived ecological data within each of the 14 regional-scale temperature- and precipitation-controlled ecological transition zones described by Osland et al. (2016, 2017*b*; see also Saenger 2002, Spalding et al. 2010). These transitions include (1) areas where winter air temperature gradients control mangrove forest structure and/or produce a regional-scale mangrove forest-to-salt marsh transition and (2) areas where precipitation gradients produce a regional-scale vegetated-to-unvegetated transition (i.e., from mangrove forests and/or salt marshes to hypersaline salt flats without vascular plants). To quantify climate–ecological linkages within a transition zone, we sought ecological data that were spatially distributed across the relevant climatic gradients. We found, however, that adequate ecological data were only readily available for the following three regions of the world: eastern North America and the Caribbean Islands (hereafter called eastern North America), eastern Australia, and western Gulf of Mexico (Fig. 2). Therefore, our analyses focus

solely on these three regions. Whereas the western Gulf of Mexico transition zone contains a precipitation-driven vegetated-to-unvegetated transition (Fig. 2*b*), the eastern North America and eastern Australia transition zones contain temperature-controlled salt marsh-to-mangrove transitions (Fig. 2*c, d*). We used climate data to identify the boundaries for each transition zone (Fig. 2*b–d*). In eastern North America and eastern Australia, the region boundaries spanned gradients in minimum air temperature from  $-40^{\circ}$  to  $20^{\circ}\text{C}$  and  $-10^{\circ}$  to  $15^{\circ}\text{C}$ , respectively. In the western Gulf of Mexico, the region boundaries spanned a mean annual precipitation gradient that ranged from 650 to 2000 mm. Within each region, we created a grid of cells with a resolution of  $0.5^{\circ}$  (i.e.,  $\sim 55$  km cell size at the equator). We converted all data (i.e., the gridded global climate data as well as the literature-derived ecological data) to this 0.5-degree resolution.

### *Climate data*

We selected the following three climatic variables for our analyses: minimum air temperature, mean annual air temperature, and mean annual precipitation. Minimum air temperature was selected as a variable due to its critical role in controlling the distribution and abundance of mangrove forests relative to salt marshes (Woodroffe and Grindrod 1991, Osland et al. 2013, Cavanaugh et al. 2014, Gabler et al. 2017); freezing and/or chilling temperatures affect plant performance and result in mangrove damage or mortality (Markley et al. 1982, McMillan and Sherrod 1986, Pickens and Hester 2011, Osland et al. 2015, 2017*a*, Lovelock et al. 2016). Minimum air temperature is a particularly important variable for quantifying the ecological thresholds associated with the mangrove–marsh transition zone (Stuart et al. 2007, Osland et al. 2013, 2017*b*). Hence, we used minimum air temperature for our temperature-focused analyses of canopy height and above-ground biomass. Mean annual air temperature was also selected as a

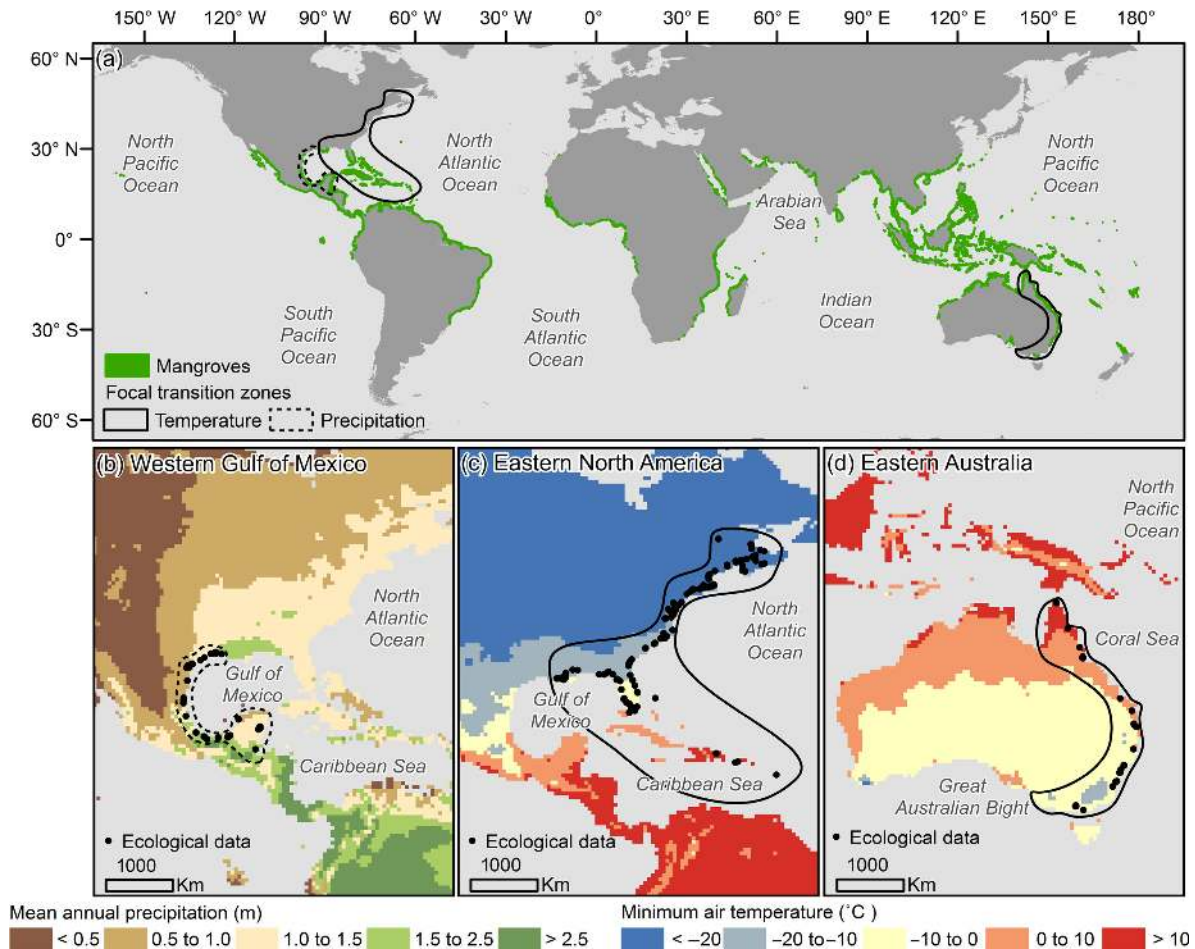


Fig. 2. Maps of global mangrove distribution (a) and mean annual precipitation (b) or minimum air temperatures (c, d) in the focal transition zones. The polygons denote the climatic transition zones evaluated in this study. Polygon line styles indicate the climatic driver hypothesized to be controlling tidal saline wetlands structure and function in each transition zone. Black dots in b–d indicate the locations of literature-derived ecological data used in our analyses.

variable due to its influence on plant and microbial physiology; mean annual temperature is directly correlated with the number of growing degree days (Appendix S1: Fig. S1) and has been shown to regulate primary productivity (Kirwan et al. 2009) and decomposition (Kirwan et al. 2014, Ouyang et al. 2017) in tidal saline wetlands. We used mean annual air temperature for our temperature-focused analyses of above-ground productivity, soil carbon density, and soil carbon accumulation. Mean annual precipitation was selected as a variable for consideration due to its critical role in controlling the abundance of

tidal saline wetland plants (Bucher and Saenger 1994, Osland et al. 2014b, Gabler et al. 2017). Low precipitation can lead to hypersaline conditions as oceanic salts accumulate, which in turn can limit vegetation establishment and performance (Zedler 1983, Pennings and Bertness 1999, Semeniuk 2013, Reef and Lovelock 2014). We used mean annual precipitation for all of our precipitation-focused analyses.

We obtained air temperature and precipitation data from gridded climate datasets. For minimum air temperature ( $T_{\min}$ ), we used multiple data sources to characterize the absolute coldest air



temperature that occurred within each 0.5-degree resolution cell across a multi-decadal period (for context, see Osland et al. 2013, Cavanaugh et al. 2014). For cells within the conterminous United States, we used 2.5-arc-min resolution data (~5 km cell size at the equator) created by the PRISM Climate Group (Oregon State University; <http://prism.oregonstate.edu>; Daly et al. 2008), for the period extending from 1981 to 2010. For continental cells outside of the United States, we used 1-degree resolution data (~111 km cell size at the equator) created by Sheffield et al. (2006), for the period extending from 1981 to 2010. For most islands outside of the conterminous United States (e.g., Caribbean and Pacific Islands), we used 0.5-degree resolution data created by Maurer et al. (2009), for the period extending from 1971 to 2000. For mean annual temperature and precipitation, we used 30-arc-second resolution (~1 km cell size at the equator) mean annual precipitation ( $P_{ma}$ ) and mean annual temperature ( $T_{ma}$ ) data from the WorldClim Global Climate Data (Hijmans et al. 2005), for the period extending from 1950 to 2000. Where necessary, climate data were resampled to match the 0.5-degree resolution of the study grids.

#### *Canopy height data*

Mangrove forest and/or salt marsh vegetation canopy height data were obtained for all three of the transition zones. While some of these data were acquired from individual studies, most of these data were obtained from the following reviews: Anderson and Treshow (1980), Saenger and Snedaker (1993), Komiyama et al. (2008), Soares et al. (2012), Rovai et al. (2016; Appendix S2: Tables S1 and S2).

#### *Above-ground biomass data*

Sufficient total above-ground biomass data were only available for the eastern North America and eastern Australia transition zones. The methods used to determine above-ground biomass data varied, and categories included in our analyses for these methods are (1) end-of-season live biomass; (2) live and dead biomass averaged over multiple months; (3) end-of-season live and dead biomass; (4) end-of-season biomass (live or dead not specified); (5) biomass derived from allometric equations; or (6) method not reported. Whereas some of these data were acquired from individual

studies, most of the data were obtained from the following reviews: Saenger and Snedaker (1993), Morrisey et al. (2007, 2010), Komiyama et al. (2008), Kirwan et al. (2009), Rovai et al. (2016; Appendix S3: Tables S1 and S2).

#### *Above-ground primary productivity data*

Adequate above-ground primary productivity data were only available for the eastern North America and eastern Australia transition zones. In addition to productivity measurements using peak standing crop and litterfall methods, other productivity measurement methods are also included in the dataset, including the methods described in Smalley (1959), Wiegert and Evans (1964), Lomnicki et al. (1968), Milner and Hughes (1968), Valiela et al. (1975), Wiegert and McGinnis (1975), and Shew et al. (1981). While some of these data were acquired from individual studies, most of these data were obtained from the following reviews: Saenger and Snedaker (1993), Komiyama et al. (2008), González Trilla et al. (2009), Morrisey et al. (2010), and Day et al. (2013; Appendix S4: Tables S1 and S2).

#### *Decomposition data*

Sufficient decomposition data were not available for any of the three transition zones.

#### *Soil carbon density and carbon accumulation data*

Soil carbon density and accumulation data were only available for the eastern North America transition zone. Soil carbon data were limited to samples collected from the upper 30 cm of the soil profile so as to capture the effects of current plant communities on soil carbon distribution and to minimize any potential influence of prior habitat shifts (Owers et al. 2016). Carbon density data were obtained from the following reviews: Chmura et al. (2003), Kristensen et al. (2008), and Ouyang and Lee (2014; Appendix S5: Tables S1 and S2). Carbon accumulation data were acquired from some individual studies, but most were obtained from the following reviews: Chmura et al. (2003) and Ouyang and Lee (2014; Appendix S6: Tables S1 and S2).

#### *Data analyses*

Cell-level means were used to convert the ecological data to the 0.5-degree resolution of the study grids. We used linear and sigmoidal

regression analyses to examine climate–ecological relationships within each transition zone. Minimum air temperature was the independent variable for analyses of canopy height and above-ground biomass in eastern North America and eastern Australia because extreme minimum temperature is the major climatic control on the distribution of mangroves relative to salt marshes in these areas. Mean annual air temperature was the independent variable for analyses of productivity, decomposition, soil carbon density, and soil carbon accumulation in eastern North America and eastern Australia because these properties have been shown to be strongly related to growing season characteristics. In the western Gulf of Mexico, mean annual precipitation was the independent variable. For sigmoidal regression analyses, the following equation was used:

$$y(x) = \frac{a}{1 + e^{-\left(\frac{x-c}{b}\right)}}$$

where  $y$  = the ecological property variable,  $x$  = the climatic variable of interest ( $T_{\min}$ ,  $T_{\max}$ , or  $P_{\text{ma}}$ ),  $a$  = the asymptote,  $b$  = the function growth rate, and  $c$  = the function midpoint. In order to identify thresholds and transition zones, we calculated the local maxima of the first derivative ( $T$ ) of each sigmoidal model, which represents the point of the maximum rate of change (i.e., inflection point). The area between the local maximum and minimum peaks of the second derivative of each sigmoidal equation was calculated in order to identify the area of the maximum rate of change (AMRC) for each transition zone (Scheffer et al. 2001, Osland et al. 2014b). From an ecological perspective, the AMRC represents a threshold zone and  $T$  represents a discrete threshold. Both values represent areas where relatively small changes in a climatic driver can trigger large ecological responses. Linear and sigmoidal regression analyses were conducted in R (R Core Team 2016). Where linear and sigmoidal results were both significant (i.e., for the canopy height and above-ground biomass analyses), the  $r^2$  values were used to select the most appropriate model (Appendix S7: Tables S1 and S2). All mapping and geospatial analyses were performed using Esri ArcGIS 10.3.1 (Environmental Systems Research Institute, Redlands, California, USA).

## RESULTS

There were significant positive sigmoidal relationships between (1) minimum air temperature and canopy height in eastern North America (Fig. 3a) and in eastern Australia (Fig. 3b); (2) mean annual precipitation and canopy height in the western Gulf of Mexico (Fig. 3c); and (3) minimum air temperature and above-ground biomass in eastern North America (Fig. 3d) and in eastern Australia (Fig. 3e; Appendix S7: Table S2). There were significant positive linear relationships between mean annual air temperature and above-ground productivity in eastern North America (Fig. 3g) and in eastern Australia (Fig. 3h; Appendix S7: Table S1). There were no significant relationships between mean annual air temperature and soil carbon density (Fig. 3m) or soil carbon accumulation (Fig. 3p) in eastern North America (Appendix S7: Tables S1 and S2). Equations for all of these relationships are provided in Tables S1 and S2 of Appendix S7.

In eastern North America, the minimum air temperature threshold zones (the AMRC for this metric, as previously defined) for canopy height and above-ground biomass were  $-6.9^\circ$  to  $4.1^\circ\text{C}$  (Fig. 3a) and  $-8.1^\circ$  to  $2.9^\circ\text{C}$  (Fig. 3d), respectively (Appendix S7: Table S2). In eastern Australia, the minimum air temperature threshold zones for canopy height and above-ground biomass were  $-4.6^\circ$  to  $2.2^\circ\text{C}$  (Fig. 3b) and  $0.2^\circ$  to  $4.8^\circ\text{C}$  (Fig. 3e), respectively (Appendix S7: Table S2). In the western Gulf of Mexico, the mean annual precipitation threshold zone for canopy height was 1308–1780 mm (Fig. 3c; Appendix S7: Table S2).

## DISCUSSION

Ecologists have long known that climatic drivers influence ecosystem structure and function in mangrove forests, salt marshes, and salt flats, and the results from this study help to quantify those climate–coastal wetland relationships. In the subsequent sections, we discuss our hypotheses and results concerning the influence of climatic drivers on each ecosystem property. We also identify critical data limitations and discuss the broader relevance of our findings, particularly in the context of climate change.

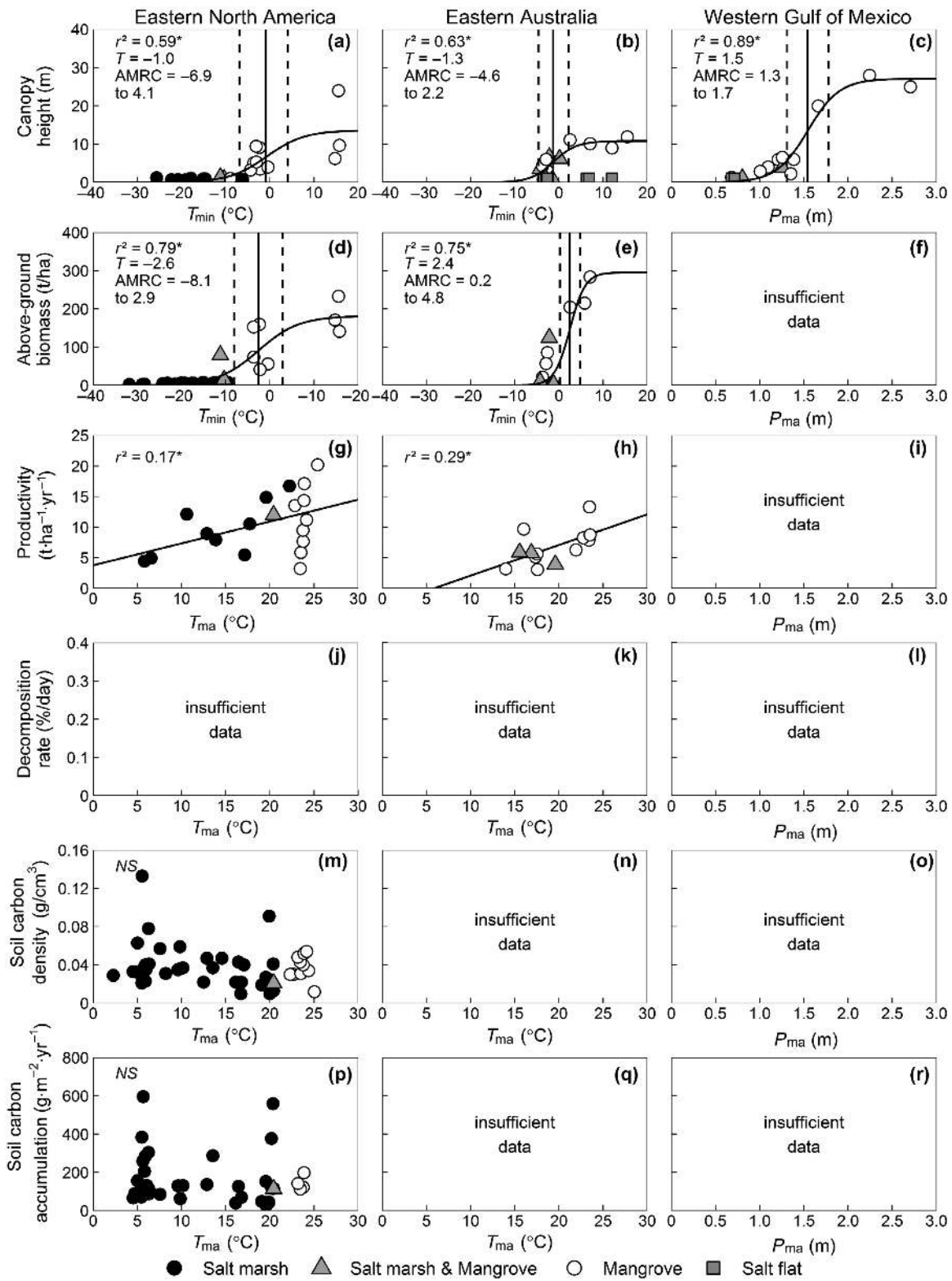


Fig. 3. The relationships between minimum air temperature ( $T_{min}$ ), mean annual air temperature ( $T_{ma}$ ), or mean

(Fig. 3. *Continued*)

annual precipitation ( $P_{ma}$ ) and canopy height (a–c), above-ground biomass (d–f), productivity (g–i), decomposition (j–l), soil carbon density (m–o), and soil carbon accumulation (p–r) across the three transition zones. In panels a–e, the discrete climate threshold ( $T$ ) is represented by a solid line and the dashed lines represent the threshold zone boundaries (i.e., the area of the maximum rate of change [AMRC]). \* $P < 0.05$ ; NS, not significant.

### ***Canopy height and above-ground biomass***

Studies focused on the mangrove–marsh ecotone in eastern North America and the temperature-driven mangrove transition zones in eastern Australia and New Zealand have shown that air temperature regimes can have a large effect on tidal saline vegetation canopy height and above-ground biomass (Lugo and Patterson-Zucca 1977, Osunkoya and Creese 1997, Morrissey et al. 2010, Osland et al. 2014a, 2015, Doughty et al. 2016, Yando et al. 2016, Gabler et al. 2017). Twilley et al. (1992), Saenger and Snedaker (1993), Alongi (2009), Twilley and Day (2012), and Sanders et al. (2016) characterized negative relationships between latitude (a temperature proxy) and mangrove forest above-ground biomass. Rovai et al. (2016) recently developed a continental-scale model for mangrove forest above-ground biomass, which includes temperature as a critical variable. In salt marshes, there are also negative latitude–biomass and latitude–height relationships (Turner 1976, Kirwan et al. 2009, McCall and Pennings 2012). Despite significant independent progress in the fields of mangrove forest and salt marsh ecology and recent studies that used field-based data from the northern Gulf of Mexico (Gabler et al. 2017) and the Atlantic coast of North America (Simpson et al. 2017), no study, to our knowledge, has evaluated temperature–height or temperature–biomass relationships using salt marsh and mangrove forest literature review-based data together. Here, we hypothesized that there are positive sigmoidal relationships between minimum air temperature and canopy height and minimum air temperature and above-ground biomass (Fig. 1a, c, respectively; Gabler et al. 2017). Our results from eastern North America and eastern Australia support these hypotheses; near poleward mangrove transition zones, there are regional, minimum temperature-controlled thresholds for canopy height and above-ground biomass in tidal saline wetlands. In terrestrial ecosystems, minimum air temperature gradients in the transition zone between tropical

and temperate climates do not produce grassland-to-forest transitions or decreases in forest height and biomass; similar climatic gradients merely produce terrestrial forest-to-forest transitions without comparable changes in height or biomass (Stegen et al. 2011, Pan et al. 2013, Liu et al. 2014). Hence, the temperature–height and temperature–biomass relationships present in tidal saline wetlands differ greatly from those relationships present in terrestrial ecosystems. These results imply that, near the tropical-to-temperate climatic transition zone, the effects of future changes in temperature regimes upon canopy height and above-ground biomass may be greater in tidal saline wetlands than in terrestrial ecosystems. The implications of these structural changes for the provision of certain ecosystem goods and services are important. For example, changes in above-ground structure will greatly affect avian habitat (Chavez-Ramirez and Wehtje 2012, Guo et al. 2017), above-ground carbon stocks (Doughty et al. 2016, Yando et al. 2016), and potentially, coastal protection processes related to wave attenuation and erosion prevention (Gedan et al. 2011, Shepard et al. 2011, Marois and Mitsch 2015, Sutton-Grier et al. 2015, Doughty et al. 2017, Kelleway et al. 2017).

Our precipitation-based hypotheses for height and biomass are similar to our temperature-based hypotheses. Across precipitation gradients, we hypothesized that there are positive sigmoidal relationships between mean annual precipitation and canopy height and mean annual precipitation and above-ground biomass (Fig. 1b, d, respectively). The hypersaline and physiologically demanding conditions present in arid and semi-arid estuaries can lead to mangrove mortality (Duke et al. 2017, Lovelock et al. 2017) and result in the development of expansive salt flat ecosystems that lack vegetation (Adam 1990, Bucher and Saenger 1994, Saenger 2002, Semeniuk 2013). Reef and Lovelock (2014), Asbridge et al. (2015), and Lovelock et al. (2016) provide valuable recent reviews of the effects of



salinity and precipitation regimes on mangrove forest structure and function. Previous studies have shown that there is a positive sigmoidal relationship between precipitation and vegetation abundance in tidal saline wetlands (Longley 1995, Montagna et al. 2011, Osland et al. 2014b, Gabler et al. 2017). Our hypothesis of a sigmoidal relationship between precipitation and canopy height was supported by our analysis of literature-derived data from the western Gulf of Mexico. We were not able to obtain sufficient biomass data across a relevant precipitation gradient to test our precipitation–biomass hypothesis. However, since biomass is correlated with height at this scale (Rovai et al. 2016), we expect that our precipitation–biomass hypothesis is also valid. In a recent study, Gabler et al. (2017) used field-collected canopy height and biomass proxy data across climatic gradients along the northern Gulf of Mexico coast to quantify sigmoidal precipitation–height and precipitation–biomass relationships. These findings reinforce the valuable precipitation gradient-focused data and discussions contained within Lot-Helgueras et al. (1975), Lugo and Patterson-Zucca (1977), Bucher and Saenger (1994), Saenger (2002), Méndez-Alonzo et al. (2008), and Yando et al. (2016). Collectively, these results are also complemented by temporal analyses showing that precipitation fluctuations, along with concomitant fluctuations in sea level in certain areas, can result in the expansion and contraction of vegetated tidal saline wetlands (Diop et al. 1997, Eslami-Andargoli et al. 2009, Rogers et al. 2014, Saintilan et al. 2014, Duke et al. 2017, Lovelock et al. 2017). In terrestrial ecosystems, there are also positive precipitation–biomass and precipitation–height linkages (e.g., across precipitation-induced desert-to-grassland-to-forest transitions; Whittaker 1970, Pan et al. 2013, Liu et al. 2014); however, due to the physically demanding and dynamic abiotic conditions present in tidal saline wetlands, we expect that the rate of ecological change across precipitation gradients may be higher in tidal saline wetlands compared to their terrestrial counterparts. Similar to changes in temperature regimes, precipitation-induced changes in above-ground biomass and canopy height would greatly influence certain ecosystem goods and services provided by tidal saline wetlands.

### *Above-ground productivity*

Temperature regimes greatly influence ecosystem productivity in terrestrial ecosystems (Churkina and Running 1998, Nemani et al. 2003, Chu et al. 2016). Despite large differences in above-ground biomass (i.e., relatively lower biomass in temperate salt marshes compared to tropical mangrove forests), mangrove forests and salt marshes both have the potential to be highly productive ecosystems under optimal physicochemical conditions (Mendelsohn and Morris 2002, Twilley and Day 2012). To our knowledge, our study is the first to use productivity data from both salt marshes and mangrove forests to characterize the influence of climatic drivers on tidal saline wetlands. In mangrove forests, Twilley et al. (1992), Saenger and Snedaker (1993), and Alongi (2009) identified negative linear relationships between latitude and above-ground productivity. In salt marshes, Turner (1976) and Kirwan et al. (2009) identified a negative linear relationship between latitude and above-ground productivity. Kirwan et al. (2009) also identified a negative linear relationship between mean annual temperature and above-ground productivity in salt marshes. Based upon these results, we hypothesized that there would be a positive linear relationship between mean annual air temperatures and above-ground primary productivity in all tidal saline wetlands (Fig. 1e). Our findings from eastern North America and eastern Australia support this hypothesis, as we identified a positive linear temperature–productivity relationship despite sigmoidal temperature–height and temperature–biomass relationships. Since the ability of coastal wetlands to adjust to sea-level rise is partly dependent upon ecogeomorphic feedbacks between inundation, plant growth, and sedimentation (Morris et al. 2002, Kirwan et al. 2010), a linear productivity response (versus a sigmoidal response) has important implications for models of coastal wetland response to sea-level rise. Whereas a sigmoidal relationship might indicate that temperature-induced mangrove forest encroachment into salt marsh may dramatically increase productivity and increase the ability of coastal wetlands to build surface elevations with progressive sea-level rise, a linear relationship might reflect minor effects of temperature-induced mangrove encroachment upon ecosystem productivity and



ecogeomorphic feedbacks relative to highly productive salt marshes (Yando et al. 2016). The significant relationships between mean annual temperatures and productivity identified for eastern North America and eastern Australia suggest that productivity will be impacted by changes in mean temperature (e.g., growing season characteristics) as opposed to changes in air temperature extremes.

Across precipitation gradients, a decrease in tidal saline wetland above-ground productivity is expected due partially to physiological stress associated with hypersaline conditions and low freshwater availability (Ibáñez et al. 2012, Reef and Lovelock 2014, Lovelock et al. 2016, Osland et al. 2016). In terrestrial ecosystems, there is a positive relationship between precipitation and productivity (Churkina and Running 1998, Knapp and Smith 2001, Chu et al. 2016). We hypothesized that there is a positive sigmoidal relationship between mean annual precipitation and above-ground productivity as highly productive mangrove forests or salt marshes would be expected to replace tidal flats or low-growing succulent-dominated marshes as the availability of freshwater increases across a rainfall gradient (Fig. 1f). Although we were unable to find sufficient productivity data across precipitation gradients to test this hypothesis, previous studies have found sigmoidal patterns for vegetation abundance across the precipitation gradient in the western Gulf of Mexico (Longley 1995, Montagna et al. 2011, Osland et al. 2014b, Gabler et al. 2017). On a physiological level, high salinities and low porewater osmotic potentials affect water uptake, transport, and loss in tidal saline wetland plants, and plant persistence during hypersaline conditions requires water acquisition adaptations that are energetically costly (Ball 1988, Callaway and Sabraw 1994, Field 1995, Naidoo 2006, Stachelek and Dunton 2013, Reef and Lovelock 2014, Nguyen et al. 2017). Whereas wetlands in arid and semi-arid regions may be resistant to minor episodes of drought, long-term changes in freshwater availability and estuarine salinity can result in mortality and significantly alter the structure and functioning of coastal wetlands (Noe and Zedler 2001, Forbes and Dunton 2006, Krauss et al. 2007, Lovelock et al. 2017). Additionally, the ecosystem impacts of future changes in precipitation regimes may be compounded by concurrent

changes in sea level and air temperatures and also by human land-use pressures resulting in altered river discharge and tidal exchange patterns (Gilman et al. 2008, McKee et al. 2012, Alongi 2015, Ward et al. 2016).

### *Decomposition*

For terrestrial ecosystems, Zhang et al. (2008) identified positive linear relationships between climatic variables (i.e., temperature, precipitation) and litter decomposition (see also Kirschbaum 1995, Davidson and Janssens 2006, García-Palacios et al. 2013). For salt flats, salt marshes, and mangrove forests, we expected a positive linear relationship between climatic variables (i.e., mean annual air temperature, mean annual precipitation) and decomposition rates (Fig. 1g, h, respectively). However, we did not have sufficient data to fully evaluate the effects of climatic drivers on decomposition. In comparison with the other ecosystem properties examined in this study, decomposition data are labor intensive and difficult to collect. In a global review of the limited root decomposition data available from tidal saline wetlands, Ouyang et al. (2017) identified significant effects of temperature, latitude, and precipitation. Support for our temperature-based hypothesis can also be found in relevant studies from salt marsh ecosystems. Craft (2007) discussed the potential edaphic effects of a positive temperature–decomposition relationship. Within temperate salt marshes that span a temperature gradient in eastern North America, Kirwan et al. (2014) identified a positive relationship between temperature and decomposition rates. In the same general region and also within salt marshes, Crosby et al. (2017) identified a negative relationship between latitude and decomposition. In an experiment within a single salt marsh in eastern North America, Kirwan and Blum (2011) identified a positive relationship between mean daily temperature and decomposition. In a west-central Florida site that contains mangrove forest and salt marsh, Lewis et al. (2014) found that higher temperatures stimulated decomposition.

We hypothesized that decomposition would be positively influenced by precipitation (Fig. 1h). The magnitude and frequency of precipitation events can modulate tidal saline wetland plant community dynamics via direct controls on freshwater availability as well as indirect effects on

estuarine salinity gradients, amount and timing of river discharge, nutrient inflows, and soil salinity and moisture (Zedler 1983, Dunton et al. 2001, Alexander and Dunton 2002). In the only study to directly examine the influence of precipitation on decomposition in a tidal saline wetland habitat, Charles and Dukes (2009) demonstrated that decomposition in a New England (USA) salt marsh was accelerated by increased precipitation and slowed by drought. However, decomposition rates in coastal wetlands are complex and influenced by many different factors (Jones et al. 2016a, Janousek et al. 2017, Stagg et al. 2017, Wu et al. 2017), and there is a need for decomposition data from coastal wetlands located in arid and semi-arid climates.

#### *Soil carbon density and accumulation*

Soil carbon stocks and accumulation rates in tidal saline wetlands are often much larger than in their terrestrial counterpart ecosystems (Donato et al. 2011, McLeod et al. 2011, Duarte et al. 2013). In a seminal contribution and one of the only global-scale studies to include ecosystem property data from both mangrove forests and salt marshes, Chmura et al. (2003) investigated patterns of soil carbon density and soil carbon accumulation; they found that soil carbon accumulation rates were similar in salt marshes and mangrove forests despite differences in soil carbon density. In a recent comparison of salt marshes and mangrove forests near the subtropical mangrove-marsh transition zone in the southeastern USA, Yando et al. (2016) found no soil carbon density differences between mangrove forests and adjacent salt marshes in areas with abundant precipitation (i.e., Louisiana and Florida; see also Perry and Mendelssohn 2009, Henry and Twilley 2013, Doughty et al. 2016). Given these findings and because we expected that productivity and decomposition vary in a positive linear fashion with temperature, we expected to find no relationship between minimum temperature and soil carbon density or soil carbon accumulation. Our results from eastern North America support these hypotheses. We expect that the lack of significant temperature-soil carbon relationships may be attributed to the following hypothesis: Temperature-driven increases in productivity (Fig. 1e) are offset by comparable temperature-driven increases in

decomposition (Fig. 1g), resulting in relatively constant carbon density and accumulation values across temperature gradients (Fig. 1i, k).

Mangrove forest expansion into salt marsh is a phenomenon that is occurring on multiple continents in diverse environmental settings in response to various environmental drivers (Saintilan et al. 2014, Saintilan and Rogers 2015). For example, changes in sea level and precipitation regimes can lead to the landward expansion of mangrove forests at the expense of salt marshes or other upslope ecosystems (Saintilan and Williams 1999, Krauss et al. 2011, Enwright et al. 2016). Similarly, changing air temperature regimes can lead to poleward mangrove expansion and salt marsh contraction (Michot et al. 2010, Cavanaugh et al. 2014, Osland et al. 2017a). In certain locations (e.g., tidal saline wetlands where marshes are dominated by succulent plants due to elevated salinity), mangrove expansion into salt marsh has resulted in elevated bulk soil carbon properties (e.g., Comeaux et al. 2012, Bianchi et al. 2013, Kelleway et al. 2016, Yando et al. 2016, Guo et al. 2017), and in certain arid coastal wetlands, soil carbon stocks can be higher in mangrove forests than in other wetland types (Schile et al. 2017). However, in wetter climates, where salt marshes are dominated by highly productive graminoids, mangrove expansion into salt marsh has typically resulted in no change in bulk soil carbon properties (Perry and Mendelssohn 2009, Henry and Twilley 2013, Doughty et al. 2016, Yando et al. 2016). In southeast Queensland (Australia), Hayes et al. (2017) found that while soil carbon stocks did not differ between mangroves and salt marshes, soil carbon stocks were strongly controlled by hydrogeomorphic setting. Using data from 84 tidal marsh sites around Australia, Macreadie et al. (2017) also show that geomorphology greatly influences soil organic carbon stocks. We highlight these differences to underscore the importance of considering differences in environmental setting when discussing the ramifications of mangrove expansion into salt marsh. The implications of mangrove expansion for below-ground ecological properties are diverse and context dependent (Howe et al. 2009, Livesley and Andrusiak 2012, Saintilan et al. 2013, Lovelock et al. 2014, Yando et al. 2016, Hayes et al. 2017). While it is tempting to generalize about the ecological effects of mangrove

encroachment into salt marsh, it is important to recognize that mangrove encroachment into salt marsh is occurring in many different settings in response to multiple drivers.

The influence of precipitation and hypersaline conditions on soil carbon cycling and storage has not received much attention in the coastal wetland literature (Osland et al. 2016, Yando et al. 2016, Schile et al. 2017). In terrestrial ecosystems, there is often a positive linear relationship between precipitation and soil carbon stocks (Burke et al. 1989, Jobbágy and Jackson 2000). Woody expansion in dryland terrestrial ecosystems can sometimes result in local increases in soil carbon (Jackson et al. 2002, Eldridge et al. 2011, Berthrong et al. 2012). Recent global-scale analyses of data from mangrove forests indicate that there is a positive relationship between precipitation and soil carbon stocks (Jardine and Siikamäki 2014, Sanders et al. 2016). Given the positive sigmoidal relationship between precipitation and vegetation abundance in tidal saline wetlands (Longley 1995, Montagna et al. 2011, Osland et al. 2014b), we hypothesized that there are positive sigmoidal relationships between mean annual precipitation and soil carbon density and soil carbon accumulation (Figs. 1j, 1 and 3). Unfortunately, ecological data from salt flats are scant, and we were not able to identify sufficient soil carbon data across precipitation gradients to test our hypotheses. However, preliminary data and support for this hypothesis are provided in Yando et al. (2016) and Schile et al. (2017), where above- and below-ground carbon stocks were lower in wetlands with lower precipitation compared to wetlands located along coastal reaches with abundant precipitation.

#### *Critical data gaps and limitations*

Ecological research in tidal saline wetlands has primarily been concentrated in areas with sufficient precipitation to support abundant salt marshes and/or mangrove forests (i.e., humid and sub-humid regions of the world). Very little research has been conducted in hypersaline tidal salt flats, which are most abundant in arid and semi-arid estuaries (Withers 2002, Semeniuk 2013, Osland et al. 2016, Gabler et al. 2017). Although we found canopy height data distributed across a precipitation gradient, we could not find sufficient ecological data to test our

hypotheses regarding the influence of precipitation upon above-ground biomass, productivity, decomposition, soil carbon density, or soil carbon accumulation. In order to advance understanding of the influence of precipitation and freshwater availability on tidal saline wetlands, ecological data are needed from tidal saline wetlands in arid and semi-arid climates (e.g., tidal salt flats, succulent-dominated salt marshes, and arid mangrove forests). Consistent and targeted data collections across regional-scale precipitation gradients would be particularly useful for testing and refining the hypothesized relationships between precipitation and wetland ecosystem properties.

In contrast to precipitation gradients, we found relevant ecological data across minimum temperature gradients in eastern North America and eastern Australia. However, additional data that are strategically collected across these gradients would help refine the identified relationships. Although we tested many of our temperature-focused hypotheses, data from temperature gradients in other regions (e.g., China, New Zealand, southern Africa, western South America) would help validate these results. To test our temperature-decomposition hypothesis, decomposition data distributed across broad temperature gradients (i.e., across tropical-to-temperate climatic transition zones) are needed.

#### *Differences between the eastern North America and eastern Australia transition zones*

There are important differences between the temperature-driven coastal wetland transition zones in eastern North America and eastern Australia. In eastern North America, winter air temperature extremes are more intense than in Australia and can cause mangrove mortality and loss of above-ground biomass (Lugo and Patterson-Zucca 1977, Stuart et al. 2007). In contrast, mangrove damage and mortality from extreme minimum temperature events in eastern Australia are very rare; however, mean winter minimum temperatures in the Australian transition zone limit mangrove performance (e.g., plant growth and reproduction; Duke 1990, Sainfilan et al. 2014, Boon 2017). Although temperature clearly affects the structure and function of mangrove forests along the eastern Australian coast, the coastline ends before mangrove forests

are fully replaced by salt marshes. As a result, *A. marina* individuals in eastern Australia are likely not at their physiological limit, and a temperature-induced mangrove-to-marsh transition zone is not clearly present (Saintilan et al. 2014). The absence of this transition affects our analyses from eastern Australia because the transition zone in eastern Australia spans a narrower and incomplete temperature gradient compared to the eastern North American transition.

In contrast, the coastal wetlands along the Gulf of Mexico and Atlantic coasts of North America provide one of the best natural laboratories in the world for investigating the effects of minimum temperature on the mangrove-marsh ecotone. Across the tropical-to-temperate climatic transition zone in eastern North America, coastal wetlands are abundant and continuously present. Moreover, precipitation regimes and the geomorphic characteristics of estuaries across this transition zone are relatively consistent, and the coastline spans the entire mangrove-to-marsh transition zone without interruption. As a result, analyses that span the temperature gradient in eastern North America can fully characterize the influence of air temperature on tidal saline wetland structure and function. In contrast, coastal wetlands in the eastern Australian transition zone are less ubiquitous and affected by concomitant hydrogeomorphic and precipitation-related factors that affect ecosystem structure and function (Saintilan and Williams 1999, Hayes et al. 2017). For example, the geomorphic characteristics of estuaries that span the temperature gradient in eastern Australia are diverse in terms of their geological setting, sedimentary environments, and hydrologic properties (Roy et al. 2001), which affect the distribution of mangrove forests, salt marshes, and salt flats.

***Beyond just climate: the role of geomorphology, tidal position, and other factors***

In this communication, we have focused primarily on the influence of climatic drivers. To simplify our message, we have intentionally avoided incorporating the influence of other important factors (e.g., geomorphology, tidal position). However, in coastal wetlands, hydrology and geomorphology are tremendously important variables that greatly influence ecosystem structure and function (Lugo and Snedaker

1974, Adam 1990, Ibáñez et al. 2012, Twilley and Day 2012, Hayes et al. 2017). Within a given wetland or estuary, inundation and salinity regimes greatly determine the position and relative abundance of mangrove forests, salt marshes, and salt flats (Eleuterius and Eleuterius 1979, Odum et al. 1982, Semeniuk 1983, Bird 1986, Rogers et al. 2006, Gabler et al. 2017). Our aim here is merely to provide a foundation for considering the role of climatic drivers in tidal saline wetlands, and we anticipate that future work will be improved via analyses that also incorporate the effects of geomorphology, tidal position, sea-level rise, atmospheric carbon dioxide concentrations, and other factors that also influence tidal saline wetland ecosystem structure and function.

## CONCLUSIONS

Climatic factors can greatly influence the structure and functioning of tidal wetland ecosystems, but most analyses have examined data from mangrove forests, salt marshes, and salt flats separately (Turner 1976, Twilley 1982, Woodroffe and Grindrod 1991, Saenger 2002). Due to constraints in data quality and access, climatic controls of ecological properties in tidal saline wetland ecosystems have not been fully elucidated. Here, we present hypotheses regarding the influence of temperature and precipitation regimes on various tidal saline wetland ecosystem properties (i.e., canopy height, biomass, productivity, decomposition, soil carbon density, soil carbon accumulation). We tested many of these hypotheses using literature-derived ecological data from mangrove forests, salt marshes, and tidal salt flats. Ecological thresholds and regime shifts are common in coastal wetlands (Scheffer et al. 2001, Folke et al. 2004). Changing winter temperature regimes can result in marsh-to-mangrove conversions (Saintilan et al. 2014), and changing precipitation regimes can result in marsh-to-salt flat or mangrove-to-salt flat conversions (Semeniuk 2013, Osland et al. 2014b, Gabler et al. 2017). Our results identify linear and nonlinear ecological effects related to these regime shifts, and advance understanding of climatic controls of ecosystem structure and function in tidal saline wetlands. Our work also highlights critical data gaps and limitations that can be improved upon via future research.



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