

# Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States

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## Abstract

We live in an era of unprecedented ecological change in which ecologists and natural resource managers are increasingly challenged to anticipate and prepare for the ecological effects of future global change. In this study, we investigated the potential effect of winter climate change upon salt marsh and mangrove forest foundation species in the southeastern United States. Our research addresses the following three questions: (1) What is the relationship between winter climate and the presence and abundance of mangrove forests relative to salt marshes; (2) How vulnerable are salt marshes to winter climate change-induced mangrove forest range expansion; and (3) What is the potential future distribution and relative abundance of mangrove forests under alternative winter climate change scenarios? We developed simple winter climate-based models to predict mangrove forest distribution and relative abundance using observed winter temperature data (1970–2000) and mangrove forest and salt marsh habitat data. Our results identify winter climate thresholds for salt marsh–mangrove forest interactions and highlight coastal areas in the southeastern United States (e.g., Texas, Louisiana, and parts of Florida) where relatively small changes in the intensity and frequency of extreme winter events could cause relatively dramatic landscape-scale ecosystem structural and functional change in the form of poleward mangrove forest migration and salt marsh displacement. The ecological implications of these marsh-to-mangrove forest conversions are poorly understood, but would likely include changes for associated fish and wildlife populations and for the supply of some ecosystem goods and services.

**Keywords:** *Avicennia germinans*, coastal wetlands, ecological thresholds, extreme events, foundation species, mangrove forest, range expansion, salt marsh, vulnerability assessment, winter climate change

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## Introduction

Foundation species are species that create habitat, modulate ecosystem dynamics, and facilitate the development of entire ecological communities (Dayton, 1972; Ellison *et al.*, 2005). Although foundation species are typically resilient organisms that play an important role in physically stressful environments (e.g., tidal wetlands, kelp forests, coral reefs, semiarid grasslands, and alpine forests) (Bertness & Callaway, 1994; Angelini *et al.*, 2011), we live in an era of unprecedented ecological change (Vitousek, 1994; Millennium Ecosystem Assessment, 2005) in which foundation species are increasingly exposed to novel and potentially adverse conditions. Natural resource managers are increasingly challenged to anticipate and prepare for the ecological effects of rapid global change (Glick, 2011). From a functional perspective, the response of foundation species to global change is especially important due to the

critical influence they have on ecosystem structure, functions, and services (Dayton, 1972; Ellison *et al.*, 2005).

In tidal saline wetlands located near tropical–temperate climate transition zones, winter climate change has the potential to cause relatively dramatic landscape-scale foundation species replacement. Salt marsh graminoids and mangrove trees (see photos in Fig. 1) are considered foundation species because they control tidal wetland ecosystem dynamics and facilitate the development of tidal saline wetland ecological communities (Teal, 1962; Bertness & Leonard, 1997; Alongi, 2009). In addition to supporting important fish and wildlife habitat, tidal saline wetland marsh and forest ecosystems improve water quality, store carbon, subsidize coastal fisheries, protect coastlines, and provide recreational opportunities (Viosca, 1928; Davis, 1940; Zedler & Kercher, 2005; Barbier *et al.*, 2011). Salt marsh and mangrove forest foundation species occupy similar tidal saline wetland geomorphic settings (Friess *et al.*, 2011), but have divergent winter climate tolerances. In tropical climates, mangrove trees often outcompete salt

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**Fig. 1** Photographs of salt marsh and mangrove forest wetlands in the Gulf of Mexico. Whereas (a), (b), and (c) are wetlands near Port Fourchon, Louisiana, (d) is a wetland in Tampa Bay, Florida.

marsh graminoids (Davis, 1940; Chapman, 1976; Tomlinson, 1986; Duke *et al.*, 1998). Salt marshes are more dominant along colder coastlines (i.e., temperate, boreal, and arctic) (Adam, 1990; Pennings & Bertness, 2001) where mangrove forests are not able to survive extreme freezing temperatures (Stuart *et al.*, 2007). The latitudinal location of salt marsh to mangrove forest transition areas is region dependent, but generally falls somewhere between 25° and 40° North or South (see discussion in Morrissey *et al.*, 2010). Near these tropical–temperate transition zones, winter climate change in the form of warmer winter temperatures and less extreme freezing events has the potential to lead to poleward mangrove forest range expansion and salt marsh displacement (Ross *et al.*, 2009; Saintilan *et al.*, 2009; McKee *et al.*, 2012).

The ecosystem goods and services provided by tidal wetlands are tightly linked to and dependent on the functional ecology and structural environment provided by tidal wetland plant foundation species. Salt marshes and mangrove forests are both highly valued ecosystems; however, salt marshes and mangrove forests support divergent ecological communities and a different suite of goods and services (Barbier *et al.*, 2011). As a result, the potential ecological implications of graminoid-to-tree conversions (i.e., salt marsh-to-mangrove forest) that are induced by winter climate change could be substantial in positive and negative ways (e.g., effects upon fish and wildlife populations, ecosystem resilience, nutrient cycling).

The southeastern United States (i.e., the US Gulf of Mexico and south Atlantic coasts) is a region of the world where the effect of mangrove forest range expansion could be substantial. Tidal saline wetlands in this region are very abundant (Field *et al.*, 1991), and this area spans a winter climate gradient that contains both salt marsh graminoid- and mangrove forest-dominated tidal saline wetlands. Despite relatively widespread awareness that winter climate extremes limit the northern distribution of mangrove forests in the southeastern United States (Davis, 1940; Lugo & Patterson-Zucca, 1977; Sherrod & McMillan, 1981; Stevens *et al.*, 2006; Ross *et al.*, 2009; Pickens & Hester, 2011; McKee *et al.*, 2012), the vulnerability of salt marshes in the region to winter climate change-induced mangrove forest migration has not been examined, and, to our knowledge, the relationship between extreme winter events and mangrove forest presence or relative abundance has not been quantified at the regional scale.

In this study, we investigated the potential for winter climate change-induced mangrove forest migration and salt marsh displacement in the southeastern United States via a 30-year observed climate record (1970–2000), mangrove forest and salt marsh presence and relative abundance data, and several alternative future winter climate scenarios. Our research addresses the following three questions: (1) What is the relationship between winter climate and the presence and abundance of mangrove forests relative to salt marshes; (2) How vulnerable are salt marshes in the region to winter

climate change-induced mangrove forest range expansion; and (3) What is the potential future distribution and relative abundance of mangrove forests under alternative future winter climate change scenarios?

## Materials and methods

### Study area and sample grid

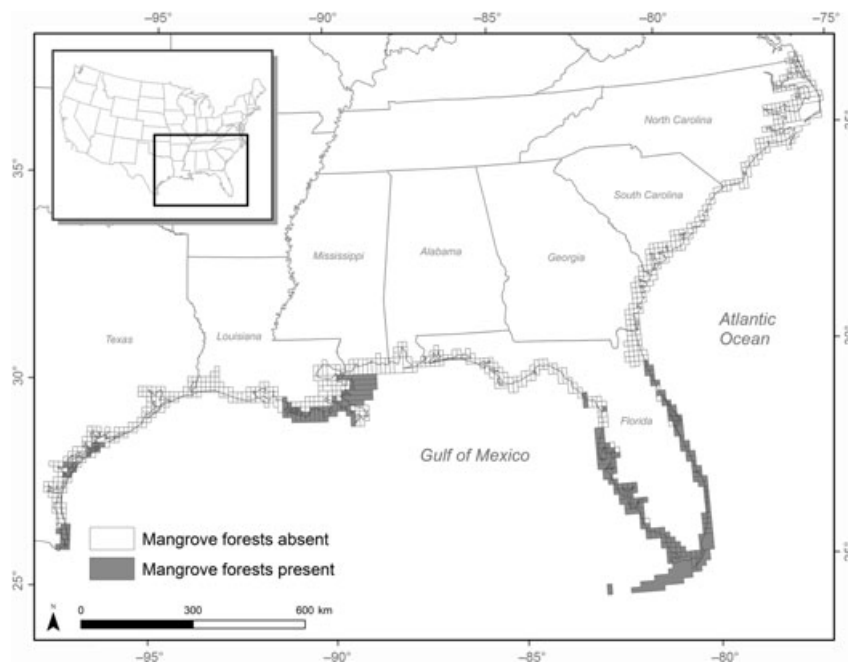
Our study area included coastal reaches of the southeastern United States that contain tidal saline wetlands (i.e., the Gulf of Mexico coast from Texas to Florida and the southern Atlantic coast from Florida to North Carolina; Fig. 2; this is an area of approximately 172,024 km<sup>2</sup>). Mangrove species in this ecoregion include *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa*, and *Conocarpus erectus*. Of these species, *A. germinans* is the most tolerant of winter extremes and has the most northern range limit. Common salt marsh species in the region include, among others, *Spartina alterniflora*, *Juncus roemerianus*, *Spartina patens*, *Salicornia virginica*, *Batis maritima*, and *Distichlis spicata*.

The study area was determined using the extent of tidal saline wetlands as determined from the US Fish and Wildlife Service National Wetlands Inventory (NWI). We established a

grid of cells within the study area for obtaining climate and coastal wetland data. Both the cell size (1/8°) and the spatial registration of the study grid match that of the gridded climate data used in the study. However, climate data from this dataset were not available for cells with open water; therefore, in some areas, 1/8° cells were merged (i.e., combined to form a larger cell). Merged cells were attributed with the data from the closest 1/8° cell for which climate data were available (Fig. 2). The resultant grid contained a total of 590 individual cells with the following size distribution (mean ± SE area in parentheses): 352 cells that contained a single 1/8° cell (166.7 ± 0.2 km<sup>2</sup>); 148 cells that contained two 1/8° cells (334.3 ± 0.7 km<sup>2</sup>); 59 cells that contained three 1/8° cells (499.1 ± 1.6 km<sup>2</sup>); 27 cells that contained four to seven 1/8° cells (819.1 ± 35.2 km<sup>2</sup>); and four cells that contained more than nine 1/8° cells (3081.3 ± 1261.8 km<sup>2</sup>).

### Coastal wetland data

We determined the salt marsh area within each cell using the estuarine emergent land cover class contained within the 2006 National Oceanic and Atmospheric Administration (NOAA) Coastal Change Analysis Program (C-CAP) dataset. We chose to use C-CAP instead of NWI to determine salt marsh area because C-CAP data are often more recent than NWI data.



**Fig. 2** Map of the study area identifying the study grid as well as the distribution of mangrove forests in the southeastern United States. Note that this map depicts mangrove forest presence not mangrove forest relative abundance and that mangrove forest presence within a cell does not imply that mangrove forests cover the entire cell area. For this analysis, we reserved the designation of mangrove forest for cells where at least a portion of the cell was covered completely by mangrove trees and not salt marsh graminoids. As a result, salt marsh-dominated areas that contain scattered mangrove individuals (e.g., Horn Island, MS, and St. Joseph Bay, FL) were not classified as mangrove forest. Data sources for this map are state specific and include: (1) the Florida Land Use and Cover Classification System (FLUCCS) (Florida Department of Transportation, 1999); (2) Michot *et al.* (2010) for Louisiana; and (3) a combination of Sherrod & McMillan (1981) and Finkbeiner *et al.* (2009) for Texas.

We determined mangrove forest presence within each cell for each of the three southeastern US states where mangrove forests are currently present (i.e., Florida, Louisiana, and Texas; Fig. 2). After evaluating the mangrove forest spatial data available for the region, we concluded that a single mangrove forest dataset for the entire study area containing the level of accuracy desired was not available; thus, we used state-level data sources for determining mangrove forest presence. A binary approach was used to quantify mangrove forest presence/absence within each cell. Whereas cells that contained mangrove forests were given a code to indicate that mangrove forests were present, cells that contained just salt marsh or areas of salt marsh with sparse mangrove individuals were given a code to indicate that mangrove forests were absent. For example, although mangrove individuals are currently present in parts of St. Joseph Bay (Florida) and on Horn Island (Mississippi), these areas were not designated as mangrove forest as mangrove individuals in those areas are scattered within a matrix that is primarily salt marsh; we reserved the designation of mangrove forest for cells where at least a portion of the cell (e.g., a 900 m<sup>2</sup> pixel) was covered completely by mangrove trees and not salt marsh graminoids. Our mangrove forest category includes mangrove forests of all heights (e.g., the stunted 1–2 m forests found in parts of Texas and Louisiana and the taller mangrove forests found in southern Florida).

For Florida, we determined mangrove forest presence using data from the 2004 Florida Land Use and Cover Classification System (FLUCCS; Florida Department of Transportation, 1999). For Louisiana, we determined mangrove forest presence using data collected via aerial surveys from a fixed-wing aircraft by Michot *et al.* (2010). For Texas, we determined mangrove forest presence via a combination of the following two data sources and our own current knowledge of the Texas coast: (1) mangrove forest distribution maps produced by Sherrod & McMillan (1981); and (2) a benthic habitat atlas of the southern and central coast of Texas produced by Finkbeiner *et al.* (2009).

For Florida, in addition to mangrove forest presence, we determined relative abundance (i.e., the percentage of tidal saline wetlands dominated by mangrove forest) by dividing the mangrove forest area (determined from 2004 FLUCCS data) by the sum of the salt marsh area and mangrove forest area contained within each cell (Fig. S1 in the Supporting Information). Relative abundance was used to determine mangrove forest or salt marsh dominance of tidal saline wetlands within a cell. Statewide mangrove forest area and relative abundance data were not available for Louisiana or Texas. Whereas the pixel resolution of the C-CAP and FLUCCS data used in this study is 30 m, the pixel resolution of the southern and central Texas NOAA benthic habitat data used in this study is variable, but generally between 0.25 and 4 m.

#### *Winter climate data*

As extreme winter temperature events are best quantified at the multidecadal scale, we chose the following two 30-year

time intervals to evaluate modern and projected future winter severity: (1) 1970–2000 (the modern climate) and (2) 2070–2100 (the projected future climate). For the modern climate, we obtained daily minimum observed temperature data for each cell from a dataset produced by Maurer *et al.* (2002). For the projected future climate, we obtained output from eight downscaled atmosphere–ocean general circulation models (AOGCMs) that were part of the World Climate Research Programme’s (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multimodel dataset (Meehl *et al.*, 2007). The output from these downscaled AOGCMs is part of a new climate dataset in development for North America for the US Geological Survey that uses a statistical asynchronous regression approach to better reflect the distribution of daily temperature extremes (Stoner *et al.*, 2012; see application and discussion of this dataset in Terando *et al.*, 2012). We obtained daily minimum temperature projections for the following eight downscaled AOGCMs for two different greenhouse gas emissions scenarios [B1 and A2; IPCC Special Report on Emissions Scenarios (Nakicenovic *et al.*, 2000)]: NCAR-CCSM3, CCMA-CGCM3.1(T47), CCMA-CGCM3.1(T63), CNRM-CM3, MPIM-ECHAM5, GFDL-CM2.0, NCAR-PCM, and BCCR-BCM2. Whereas the B1 projections represent a low greenhouse gas emissions scenario with a more convergent world, lower population growth, reduced fossil fuel use, and the adoption of less energy and material-intensive activities, the A2 projections represent a medium-high greenhouse gas emissions scenario where the world is heterogeneous, economic growth is uneven, population growth is high, and fossil fuels continue to be the dominant energy source (Nakicenovic *et al.*, 2000). The pixel resolution of the climate data used in this study is 1/8°.

#### *Linkages between winter climate and mangrove forest presence and relative abundance*

Prior to developing mangrove forest distribution and relative abundance models, we calculated various measures of winter severity for the modern climate (Table 1). To minimize the influence of unmeasured abiotic factors in the coastal wetland presence and relative abundance data, we removed all cells that were located in sections of the coast without expansive wetland areas (defined as cells containing less than two percent tidal saline wetlands). This process resulted in a modern climate–coastal wetland data matrix that contained 391 cells (i.e., 199 cells were removed from the dataset because tidal saline wetlands were less abundant in those areas). To quantify the relationship between mangrove forest presence and modern climate winter severity, we developed logistic regression models for the winter severity variables in Table 1. As Spearman rank correlation tests indicated a high degree of collinearity between these variables (the mean and minimum of the bivariate Spearman rank correlation coefficients were 0.92 and 0.76, respectively), we developed single-predictor models and selected the model that best predicted mangrove forest presence using Akaike Information Criterion (AIC). To quantify the relationship between mangrove forest relative abundance and winter severity, a data matrix from Florida that contained

**Table 1** Logistic and nonlinear regression model results for predicting mangrove forest presence and relative abundance, respectively, using winter severity variables. Relative abundance models predict the percentage of tidal saline wetlands dominated by mangrove forests.

Variable	Mangrove forest presence					Mangrove forest abundance			
	AIC	<i>a</i>	<i>b</i>	<i>a</i> Wald $\chi^2$	<i>b</i> Wald $\chi^2$	$R^2$	<i>a</i>	<i>b</i>	<i>c</i>
Mean annual minimum temperature	191.3§	4.84	1.41	36***	56***	0.85‡***	75***	0.18**	-1.75***
Mean annual maximum number of consecutive days with minimum temperature <0°C	199.9§	5.18	-2.24	51***	71***	0.85‡***	75***	-0.07*	1.51***
Minimum temperature	210.0§	8.76	0.87	42***	55***	0.82‡***	74***	0.50**	-6.97***
Mean annual minimum monthly mean temperature	210.2§	-13.69	1.09	77***	65***	0.84‡***	74***	0.26**	14.76***
Mean annual maximum number of consecutive days with minimum temperature <-6.7°C	211.6§	2.74	-9.42	40***	74***	0.79‡***	70***	10.04***	NA
Mean annual number of days with minimum temperature <0°C	226.8§	2.48	-0.46	42***	72***	0.85‡***	75***	-0.11**	2.25***
Maximum number of consecutive days with minimum temperature <0°C	240.0§	6.63	-1.25	42***	54***	0.63†***	167***	0.37***	NA
Maximum number of consecutive days with minimum temperature <-6.7°C	262.9§	2.61	-1.36	36***	82***	0.78†***	71***	1.23***	NA

†denotes an exponential decay model ( $y = a \times e^{-(b \times x)}$ ).

‡denotes a sigmoidal model ( $y = a / (1 + e^{-(x-c)/b})$ ).

§denotes a logistic model ( $y = (e^{(a+b \times x)}) / (1 + (e^{(a+b \times x)}))$ ).

AIC is an abbreviation for Akaike Information Criterion.

Wald  $\chi^2$  is the Wald chi-square statistic shown for the *a* and *b* coefficients of the logistic models.

\* $P < 0.05$

\*\* $P < 0.01$

\*\*\* $P < 0.001$ .

101 cells was used to develop sigmoidal or exponential decay regression models for the winter severity variables in Table 1. To identify temperature thresholds for mangrove replacement of salt marsh, we used two approaches: (1) a sigmoidal regression approach where the inflection point of a sigmoidal model was determined as a threshold; and (2) a recursive partitioning approach where the first node of a regression tree was determined as a threshold. To identify temperature thresholds for mangrove forest presence, we used a recursive partitioning approach where the first node of a classification tree was determined as a threshold. Recursive partitioning was conducted in R (<http://cran.r-project.org>) using the Rpart package (Therneau & Atkinson, 1997), sigmoidal and exponential decay regression analyses were conducted in Sigma Plot Version 12.0 (Systat Software, Inc., San Jose, CA, USA), and logistic regression analyses were conducted in SAS Version 9.1.3 (SAS Institute, Cary, NC, USA) using the LOGISTIC procedure (i.e., PROC LOGISTIC). Maps were created using ArcGIS 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA, USA).

#### *Salt marsh vulnerability to mangrove forest migration: evaluating future scenarios*

Mean annual minimum temperature (MAMT) was identified as the winter climate variable that best predicted mangrove forest presence and relative abundance (see  $R^2$  and AIC in Table 1). We used the modern climate-coastal wetland models for MAMT (Table 1) to predict the future probability of mangrove forest presence and relative abundance under two types of future climate scenarios: (1) region-wide single-value warming scenarios ranging from 0 °C to 8 °C; and (2) AOGCM-based future climate projections (i.e., eight AOGCM projections for 2070–2100 for two emissions scenarios).

For the region-wide single-value warming scenarios, we evaluated the effect of temperature increases ranging from 0 °C to 8 °C (i.e., increases in temperature relative to the modern climate MAMT) upon mangrove forest relative abundance. For each cell, we also determined the temperature increase that would be required to reach the MAMT threshold temperature (Table 2) required for mangrove forest domi-

**Table 2** Winter temperature thresholds for predicting mangrove forest presence in and dominance of tidal saline wetland habitat. Threshold values and the accompanying complexity parameters (identified in parentheses) were determined via recursive partitioning

Variable	Presence	Dominance
Mean annual minimum temperature	-3.0 (0.63)	-1.7 (0.84)
Mean annual maximum number of consecutive days with minimum temperature <0°C	2.2 (0.60)	1.5 (0.85)
Minimum temperature	-8.9 (0.64)	-7.0 (0.81)
Mean annual minimum monthly mean temperature	13.6 (0.64)	14.9 (0.83)
Mean annual maximum number of consecutive days with minimum temperature <-6.7°C	0.2 (0.60)	0.0 (0.76)
Mean annual number of days with minimum temperature <0°C	3.7 (0.59)	2.2 (0.85)
Maximum number of consecutive days with minimum temperature <0°C	4.5 (0.48)	4.5 (0.80)
Maximum number of consecutive days with minimum temperature <-6.7°C	1.5 (0.57)	0.5 (0.76)

nance (i.e., for each cell, we calculated the difference between the MAMT threshold for mangrove dominance and the modern climate MAMT). We used the resultant data to illustrate salt marsh vulnerability to mangrove forest migration and determine the amount of salt marsh area within each state that would potentially be affected by region-wide single-value temperature warming scenarios ranging from 0 °C to 8 °C.

For the AOGCM-based future climate scenarios (i.e., eight AOGCM projections for 2070–2100 for two emissions scenarios), we determined the projected MAMT for each cell. Then, we derived an ensemble of MAMT projections for each of the two emissions scenarios (A2 and B1) by calculating the mean and standard error of the eight AOGCMs for each emissions scenario. We used these ensemble temperature projections and the mangrove forest distribution and relative abundance models to evaluate future mangrove forest presence and future mangrove forest relative abundance in each cell for each of the two emissions scenarios (A2 and B1).

## Results

### *Linkages between winter climate and mangrove forest presence and relative abundance*

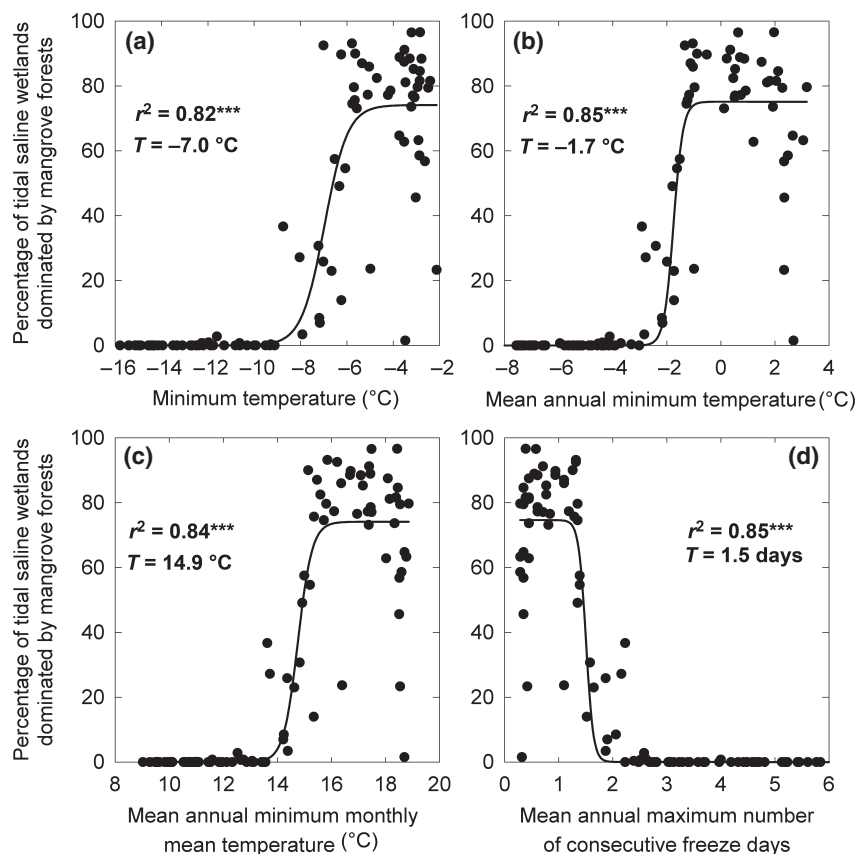
There was a strong relationship between all eight winter severity variables and mangrove forest presence and relative abundance (Table 1; Fig. 3). In addition to

presenting mangrove forest distribution and relative abundance models for each of the variables (Table 1), we identified threshold levels for predicting mangrove forest presence and relative abundance (Table 2; Fig. 3). For example, the 30-year minimum temperature thresholds for mangrove forest presence and dominance were identified as -8.9 °C and -7.0 °C, respectively (Table 2; Fig. 3a). Note that for all of the winter severity thresholds, the threshold for mangrove forest presence is lower (i.e., colder) than for mangrove forest dominance.

### *Salt marsh vulnerability to mangrove forest migration*

Using the modern climate MAMT-based mangrove forest distribution and relative abundance models (Table 1; Fig. 3b), we evaluated salt marsh vulnerability to mangrove forest migration under alternative winter climate change scenarios (Figs 4–6). The region-wide single-value warming scenarios illustrate the sensitivity of salt marsh habitat to MAMT increases relative to the modern climate and quantify the amount of salt marsh area within each state that would become vulnerable to mangrove forest replacement under MAMT warming scenarios ranging from 0 °C to 8 °C (Figs 4 and 5). Our results indicate that, within the region, salt marshes in Louisiana, Texas, and Florida are most vulnerable to winter climate change-induced mangrove forest range expansion; for example, with a 2 °C to 4 °C increase in MAMT, 6820 (95% of LA state total), 1970 (100% of TX state total), and 830 (60% of FL state total) km<sup>2</sup> of salt marsh could become vulnerable to mangrove forest replacement (Figs 4 and 5a). Within the Gulf of Mexico, salt marshes in Mississippi, Alabama, and parts of the northwest Florida coast (i.e., much of the area north and west of Cedar Key, FL) are the least sensitive to winter climate change-induced mangrove forest migration as a 4 °C to 6 °C increase in MAMT relative to the modern climate would be required for salt marsh-to-mangrove forest conversions to occur (Figs 4 and 5). Along the Atlantic coast, all of the salt marshes in Georgia (1480 km<sup>2</sup>; 100% of state total) and many of the salt marshes in South Carolina (890 km<sup>2</sup>; 63% of state total) could become vulnerable to mangrove forest replacement with a 4 °C to 6 °C increase in MAMT relative to the modern climate (Figs 4 and 5a). In North Carolina, the coldest state within our study area, our results indicate that mangrove forest replacement of salt marsh would require MAMT increases greater than 6 °C (Figs 4 and 5b).

In addition to the region-wide warming scenarios (Figs 4 and 5), we also assessed the future probability of mangrove forest presence and relative abundance under ensemble B1 and A2 future climate projections



**Fig. 3** The relationship between mangrove forest relative abundance (i.e., the area-based percentage of tidal saline wetlands that are dominated by mangrove forests) and four winter severity variables: (a) minimum temperature, (b) mean annual minimum temperature, (c) mean annual minimum monthly mean temperature, and (d) mean annual maximum number of consecutive freeze days. Tidal saline wetland areas that are not dominated by mangrove forests are dominated by salt marshes. T denotes a threshold for salt marsh and mangrove forest transitions determined via recursive partitioning.

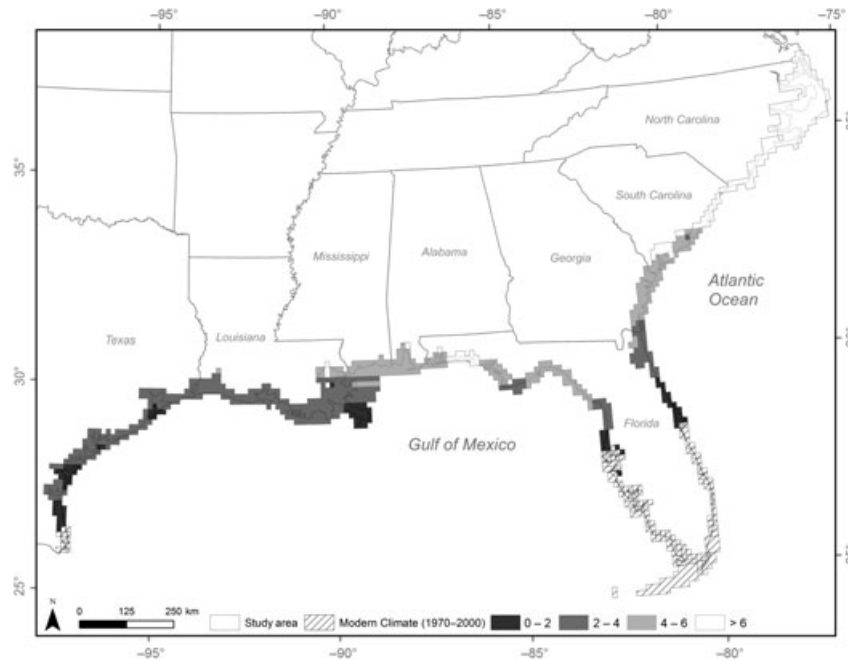
(Fig. 6). The ensemble projected MAMT increases across the study area ranged from a 0 °C to 1 °C increase for some cells under the B1 scenario up to a 6 °C increase for some cells under the A2 scenario (Fig. S2 in the Supporting Information). Whereas the ensemble B1 projection suggests a mean  $\pm$  SE MAMT increase of 2.3 °C  $\pm$  0.4 °C, the ensemble A2 projection suggests a mean  $\pm$  SE MAMT increase of 4.3 °C  $\pm$  0.5 °C across all cells and AOGCM projections (Fig. S2 in the Supporting Information). Although both scenarios predict an expansion of mangrove forests and displacement of salt marsh, the total salt marsh area affected by mangrove forest expansion is greater in the A2 scenario than in the B1 scenario (Fig. 6) due to the higher temperature projections accompanying the higher emissions scenario (Fig. S2 in the Supporting Information).

## Discussion

Ecologists have long noted that extreme winter events influence the distribution and abundance of salt

marshes and mangrove forests (Storey & Gudger, 1936; Davis, 1940; Lugo & Patterson-Zucca, 1977; McKee *et al.*, 2012). However, due to the limited availability of winter climate and coastal wetland occurrence and abundance data, most investigations of winter climate controls upon mangrove–salt marsh interactions have been based on: (1) local-scale observations of mangrove forest structural effects or mortality during extreme winter events (Davis, 1940; Lugo & Patterson-Zucca, 1977; Kangas & Lugo, 1990; Stevens *et al.*, 2006; Ross *et al.*, 2009; Pickens & Hester, 2011); or (2) global-scale evaluations of the distribution of mangrove forests relative to mean monthly or mean annual air or sea surface temperature data (Chapman, 1976; Tomlinson, 1986; Duke *et al.*, 1998).

In this study, we used extreme winter temperature data (i.e., extremes of the daily minima) to develop regional-scale mangrove forest distribution and relative abundance models for the southeastern United States. These simple models (Tables 1 and 2; Fig. 3) can be used to predict mangrove forest presence or relative



**Fig. 4** This map shows the increase in mean annual minimum temperatures ( $^{\circ}\text{C}$ ) relative to the modern climate (1970–2000) that is expected to lead to mangrove forest dominance of tidal saline wetland habitats relative to salt marshes. The modern climate category reflects areas where mangrove forests are currently expected to be dominant relative to salt marshes. Note that these analyses apply just to the tidal saline wetland habitat within each cell and not the entire cell.

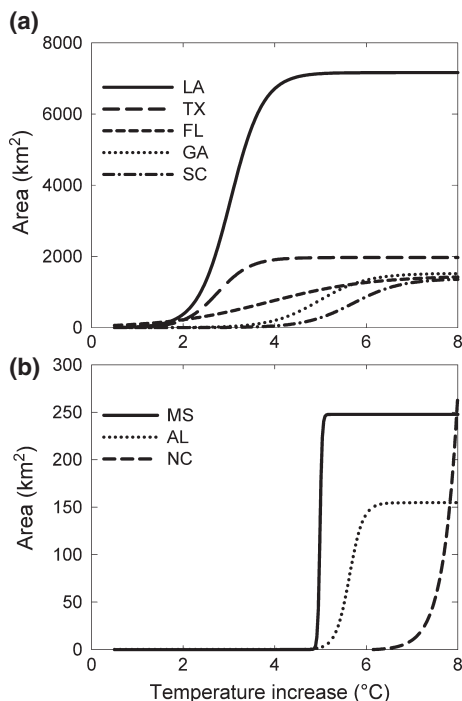
abundance using global climate model projections of future winter temperatures (e.g., Figs 4–6). Of the winter severity variables examined, MAMT and the 30-year minimum temperature are among the most useful and relevant from a physiological and logistical perspective. MAMT is frequently used at regional scales to illustrate plant tolerance of winter climate extremes (e.g., the US Department of Agriculture Plant Hardiness Zone Maps); the freeze tolerance of many plant species matches the MAMT at their poleward range limit (Sakai & Weiser, 1973; Woodward, 1987; Kreyling, 2010).

Our 30-year minimum temperature threshold analyses indicate that mangrove forests in the southeastern United States are not likely to be present in areas where minimum temperatures fall below approximately  $-8.9^{\circ}\text{C}$ , and mangrove forests are not likely to be dominant in areas where minimum temperatures fall below approximately  $-7.0^{\circ}\text{C}$  (Table 2; Fig. 3a). In his seminal treatise on South Florida mangroves, John Henry Davis identified a minimum temperature threshold level for mangrove forests that is close to but slightly warmer than the mangrove forest presence threshold we identified; based on historical observations, Davis (1940) speculated that temperatures below  $-4^{\circ}\text{C}$  would be required for mangrove mortality to occur. More recently, Stevens *et al.* (2006) observed that due to a freeze event of  $-8^{\circ}\text{C}$  near Cedar Key (Florida) in 1996,

*A. germinans* trees lost some or all of their leaves, but recovered within the year. In Texas, severe freeze events with minimum temperatures of  $-8.8^{\circ}\text{C}$  and  $-8.9^{\circ}\text{C}$  in 1983 and 1989, respectively, caused widespread *A. germinans* damage (Lonard & Judd, 1991) and mortality; these two freeze events reduced mangrove aerial coverage by 95% and 98%, respectively (Everitt *et al.*, 1996). Extreme winter events that affect mangrove forests also typically affect citrus trees and many other warm-temperate/subtropical plant species (Lonard & Judd, 1991; Rogers & Rohli, 1991; Stevens *et al.*, 2006; Saintilan *et al.*, 2009). The minimum temperature thresholds we identified for mangrove forest presence and dominance fall within the range of values reported for citrus species; minimum temperature thresholds for many citrus tree species in Florida are between  $-4.5^{\circ}\text{C}$  and  $-9^{\circ}\text{C}$  (Wiltbank & Oswalt, 1987).

Our model results for the modern climate indicate that many northern Gulf of Mexico sites where mangrove expansion into salt marsh has been investigated [e.g., Cedar Key (Stevens *et al.*, 2006); Port Fourchon (Louisiana) (Penfound & Hathaway, 1938; Patterson, 1991; Patterson & Mendelssohn, 1991; Patterson *et al.*, 1993, 1997; Perry, 2007; Perry & Mendelssohn, 2009; Alleman & Hester, 2011a,b; Pickens & Hester, 2011; Krauss *et al.*, 2012), Galveston (TX) (Comeaux *et al.*, 2012), and Port Aransas (TX) (McMillan, 1971; Sherrod





**Fig. 5** The winter climate-dependent vulnerability of salt marshes to displacement by mangrove forests in: (a) the states of Louisiana, Texas, Florida, Georgia, and South Carolina; and (b) the states of Mississippi, Alabama, and North Carolina. This figure reflects the amount of salt marsh area that could be converted into mangrove forest within each state in response to increases in mean annual minimum temperature (°C) relative to the modern climate (1970–2000). See text for additional description.

& McMillan, 1981; Everitt *et al.*, 1996; Chavez-Ramirez & Wehtje, 2012; Comeaux *et al.*, 2012)] are in or proximate to areas where mangrove forests are currently predicted to be present but not dominant relative to salt marshes (i.e., where small *A. germinans* forests and individuals are present within a matrix that is primarily dominated by salt marsh graminoids).

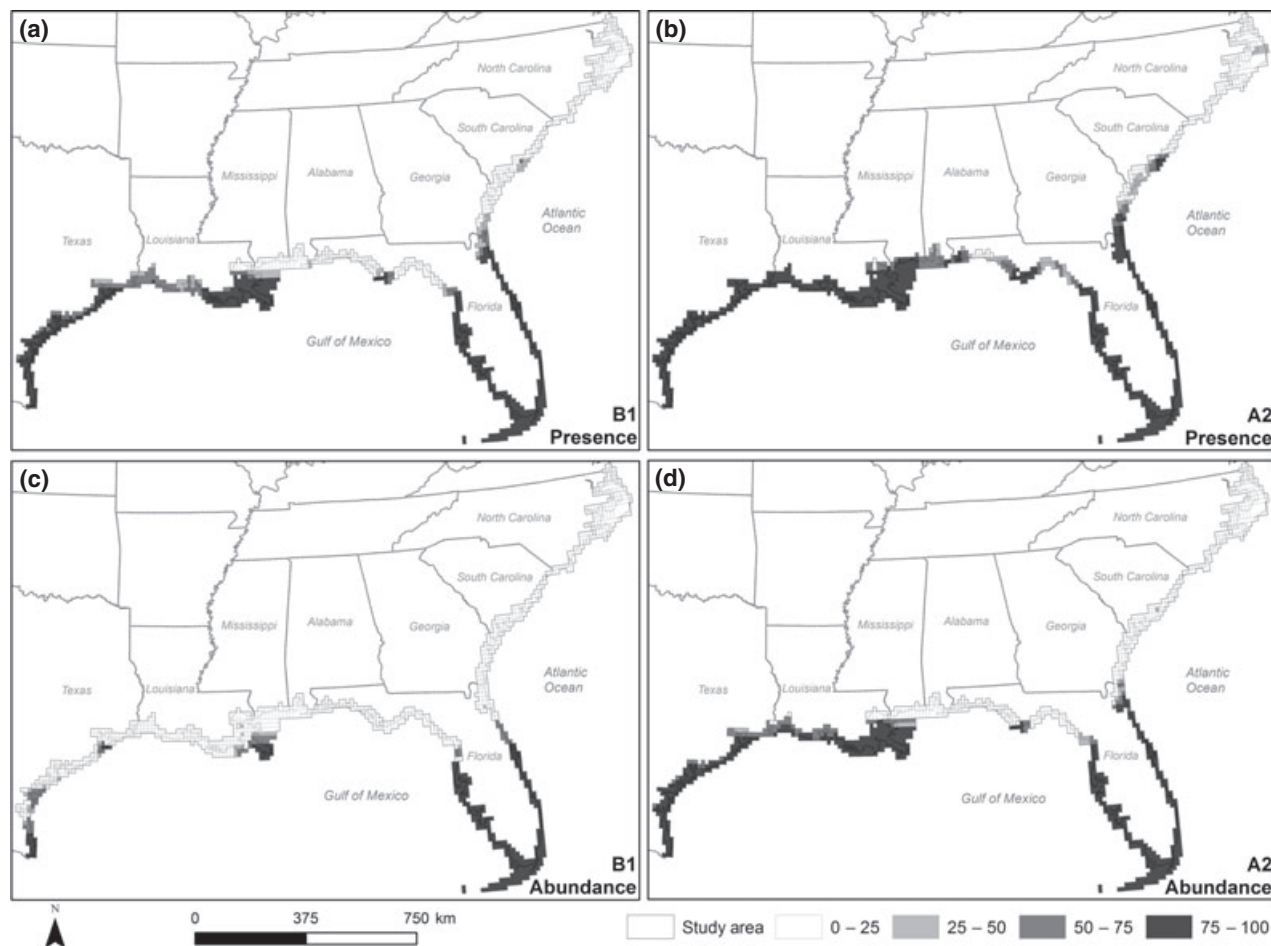
One of our primary study objectives was to evaluate the vulnerability of salt marshes in the southeastern United States to mangrove forest range expansion under alternative future winter climate scenarios. Climate change vulnerability assessments can be conceptually divided into three elements: sensitivity, exposure, and adaptive capacity (Glick, 2011). We determined the sensitivity of mangrove forests to extreme winter climate events that lead to mortality and/or affect forest structural development. We also determined the sensitivity of salt marshes to winter climate change that could enable mangrove forest range expansion and salt marsh displacement. Our analyses indicate that salt marshes in the states of Louisiana, Texas, and parts of Florida are especially sensitive to

winter climate change due to their proximity to the winter climate threshold that differentiates between mangrove forest and salt marsh dominance. For example, with a 0 °C to 2 °C increase in MAMT relative to the modern climate, approximately 740 km<sup>2</sup> (7%) of salt marsh in these three states would likely become susceptible to mangrove expansion, and with a 2 °C to 4 °C increase in MAMT relative to the modern climate, approximately 9860 km<sup>2</sup> (93%) of salt marsh in these three states would likely become susceptible to mangrove expansion (Figs 4 and 5a; values in parentheses represent the percentage of the total salt marsh area in these three states). We used alternative winter climate scenarios to evaluate the potential exposure of coastal wetlands in the region to winter climate change. Our analyses of statistically downscaled future climate projections for 2070–2100 indicate that the potential for mangrove forest range expansion would be moderate under a lower greenhouse gas emissions scenario (B1), but relatively high under a medium-high greenhouse gas emissions scenario (A2) (Fig. 6).

Implicit in our evaluations of potential mangrove expansion under alternative future winter climate scenarios are several assumptions regarding the adaptive capacity of mangrove forests. We assume that mangrove forests will be able to migrate relatively rapidly in response to winter climate change. For many terrestrial plant species, observed migration in response to climate change can be slow and/or unpredictable due to multiple factors including limited dispersal capacity, negative interactions with species already present in newly available habitat, and unsuitable nonclimatic abiotic conditions (Pitelka, 1997; Clark *et al.*, 2003; Ibáñez *et al.*, 2009; Araújo & Peterson, 2012; Zhu *et al.*, 2012).

However, we expect that range migration for some mangrove species would occur more rapidly than for most terrestrial plant species. Water-dispersed plants are often capable of traveling longer distances than plants that are wind or animal dispersed (Ridley, 1930), and many mangrove species produce water-dispersed salt-tolerant propagules which float and are viable for extended periods (Rabinowitz, 1978; Tomlinson, 1986; Alleman & Hester, 2011b). As a result, tropical storms and/or oceanic currents can transport viable mangrove propagules of some species across relatively large distances (Davis, 1940; Gunn & Dennis, 1973; Clarke, 1993; Nettel & Dodd, 2007; Sousa *et al.*, 2007).

With regards to biotic interactions in newly suitable habitats, we assume that competition between mangroves and salt marshes will be most intense in areas near the poleward range limit of mangrove forests where extreme winter climate limits mangrove forest growth and development (i.e., areas where our models indicate that mangrove forests are likely to be present



**Fig. 6** Predictions of mangrove forest presence and relative abundance (i.e., percentage of tidal saline wetlands dominated by mangrove forests) under alternative future (2070–2100) winter climate projections: (a) probability of mangrove forest presence with an ensemble B1 scenario climate; (b) probability of mangrove forest presence with an ensemble A2 scenario climate; (c) mangrove forest relative abundance with an ensemble B1 scenario climate; and (d) mangrove forest relative abundance with an ensemble A2 scenario climate. Note that these predictions apply just to the tidal saline wetland habitat within each cell and not the entire cell.

but not dominant), but that mangrove forests will be competitively dominant in areas with warmer winters (Kangas & Lugo, 1990; Fig. 3). Although salt marsh graminoids have been shown to compete with mangrove trees in certain situations (e.g., Patterson *et al.*, 1993; McKee & Rooth, 2008; Smith *et al.*, 2009; Zhang *et al.*, 2012), several studies have indicated that, in climatically suitable areas (e.g., areas warm enough to support mature and dominant mangrove forests), salt marsh species can facilitate mangrove forest establishment and development via propagule entrapment and improved soil physicochemical conditions (Lewis & Dunstan, 1975; Lewis *et al.*, 2005; Milbrandt & Tinsley, 2006; McKee *et al.*, 2007; Smith *et al.*, 2009; Osland *et al.*, 2012; Peterson & Bell, 2012).

In terms of the suitability of abiotic conditions in newly available habitat, we make the assumption that the abiotic conditions that determine the relative

abundance of mangrove forests in Florida will be similar in other parts of the southeastern United States. For most of the region, this assumption is probably appropriate; however, in areas with very low precipitation (e.g., arid parts of southwest Texas) or continuous freshwater flow (e.g., parts of Louisiana), the abundance of mangrove forests relative to unvegetated tidal flats and/or salt marshes will likely be different (Dunton *et al.*, 2001; Montagna *et al.*, 2007). The effect of winter climate change could also be influenced by the frequency and timing of drought events; a recent study conducted in Louisiana indicates that decreased water use by *Avicennia*-dominated mangrove forests relative to *Spartina*-dominated salt marshes may provide mangrove forests with greater stress tolerance and/or a competitive advantage in some situations (Krauss *et al.*, 2012).

The simple distribution and relative abundance models we developed are intended to provide an initial

assessment of the potential for winter climate change-induced mangrove forest poleward range expansion and salt marsh displacement in the southeastern United States. There are many assumptions and uncertainties inherent to species distribution models (Wiens *et al.*, 2009), and our analyses were constrained by various factors including the availability of mangrove forest presence and abundance data, the resolution of coastal wetland data (i.e., 30 m for much of the study area), and the resolution and extent of coastal winter climate data (i.e., 1/8° resolution and no data over cells with open water, respectively). Our analyses of future projected climate data are also constrained by limitations associated with statistical downscaling (e.g., the assumption of stationarity, an unchanging envelope of variability) (Wilby & Wigley, 1997; Milly *et al.*, 2008; Wilby & Fowler, 2010). As better data become available, we expect that these models will be refined and additional complexity will be added including species-specific responses (e.g., differential winter climate responses between *A. germinans*, *R. mangle*, and *L. racemosa*) (Markley *et al.*, 1982; Ross *et al.*, 2009), biotic interactions, temperature exposure assessments (e.g., Pickens & Hester, 2011), interactions with other aspects of climate change (e.g., precipitation change, sea level rise, increasing CO<sub>2</sub>, saltwater intrusion, hydrologic alterations) (McKee & Rooth, 2008; McKee *et al.*, 2012), and mechanistic ecosystem development simulations (Doyle *et al.*, 2003, 2010; Berger *et al.*, 2008). Interactions between sea level rise and winter climate change are particularly important; whereas warming is expected to enable poleward mangrove forest migration and salt marsh displacement, sea level rise is expected to result in landward mangrove forest migration and tidal freshwater forested wetland displacement (Doyle *et al.*, 2010; Krauss *et al.*, 2011). In this study, our analyses focused exclusively on the southeastern United States; however, given the availability of global mangrove distributional data (e.g., Giri *et al.*, 2011), a global evaluation of winter climate controls upon salt marsh–mangrove forest interactions is likely feasible and would enable interregional comparisons.

Collectively, our analyses quantify the relationship between extreme winter climate events and the distribution and relative abundance of mangrove forests relative to salt marshes in the southeastern United States. The simple distribution and relative abundance models we developed can be used to gauge the potential effect of alternative future winter climate scenarios upon coastal wetlands. Our results indicate that salt marshes in Louisiana, Texas, and parts of Florida are particularly vulnerable to winter climate change-induced mangrove forest range expansion (Fig. 4). The transition from salt marsh to mangrove forest is relatively

dramatic to even the casual observer (i.e., an ecosystem that has been historically grass or herbaceous plant-dominated transitions to a forest). From an ecological perspective, the replacement of coastal wetland foundation species would likely have substantial functional and structural repercussions (Dayton, 1972; Ellison *et al.*, 2005; Osland *et al.*, 2012). The potential ecological effects of mangrove forest migration and salt marsh displacement are likely diverse, ranging from important biota effects (e.g., changing habitat for fish and birds) to ecosystem stability (e.g., habitat loss; response to sea level rise and drought; coastal protection from storms) to biogeochemical processes (e.g., carbon and nitrogen cycling; water quality improvement). Many of the important questions regarding the potential effects of mangrove forest replacement of salt marsh have not yet been fully investigated.

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### Supporting Information

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

**Fig. S1.** Mangrove forest relative abundance (i.e., the area-based percentage of tidal saline wetlands dominated by mangrove forests) in Florida.

**Fig. S2.** Mean annual minimum temperature (MAMT) differences (°C) between the modern climate (1970–2000) and two projected future climates (2070–2100): ensemble B1 and A2 scenario climates. Whereas (a) and (b) show the mean differences for the B1 and A2 scenarios, respectively, (c) and (d) show the standard error of the differences for the B1 and A2 scenarios, respectively.

**Fig. S3.** Thirty-year minimum daily temperatures (°C) across the study area for the modern climate (1970–2000).