



# Frequency of extreme freeze events controls the distribution and structure of black mangroves (*Avicennia germinans*) near their northern range limit in coastal Louisiana

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## Abstract

**Aim:** Climate change is expected to result in the tropicalization of coastal wetlands in the northern Gulf of Mexico, as warming winters allow tropical mangrove forests to expand their distribution poleward at the expense of temperate salt marshes. Data limitations near mangrove range limits have hindered understanding of the effects of winter temperature extremes on mangrove distribution and structure. Here, we investigated the influence of extreme freeze events on the abundance, height and coverage of black mangroves (*Avicennia germinans*) near their northern range limit in Louisiana.

**Location:** Coastal Louisiana, USA.

**Methods:** We quantified the relationships between the frequency of extreme freeze events and *A. germinans* abundance, height and coverage using: (a) mangrove observation points recorded via aerial surveys from a fixed-wing aircraft; (b) 30 years of temperature data; and (c) mangrove mortality and leaf damage temperature thresholds. We used freeze frequency data and mangrove–climate relationships to evaluate and spatially depict the risk of *A. germinans* freeze damage across Louisiana.

**Results:** We identified strong negative relationships between the frequency of extreme freeze events and *A. germinans* abundance, height and coverage. *Avicennia germinans* is most abundant, tall and continuous along the south-eastern outer coast of Louisiana, where the frequency of extreme freeze events is reduced (i.e., lower risk of mangrove freeze damage) by the buffering effects of comparatively warm Gulf of Mexico waters. Conversely, the risk of *A. germinans* freeze damage has historically been very high across Louisiana's Chenier Plain and within more inland wetlands in the Deltaic Plain.

**Main conclusions:** Our analyses advance understanding of how the frequency of extreme freeze events controls the distribution, height and coverage of *A. germinans* near its northern range limit. In addition to informing climate-smart coastal restoration efforts, our findings can be used to better anticipate and prepare for the tropicalization of temperate wetlands due to climate change.

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## KEYWORDS

*Avicennia germinans*, black mangrove, climate change, coastal wetland, freezing, Louisiana, mangrove, range limit, salt marsh, temperature

## 1 | INTRODUCTION

In the face of rapid climate change, ecologists and natural resource managers are increasingly challenged to better anticipate and prepare for the effects of changing temperature and precipitation regimes on the distribution of species, ecosystems and biomes (Pecl et al., 2017; Scheffers et al., 2016; Thomas, 2010). Near the transition between tropical and temperate climates, warming air and ocean temperatures are expected to allow tropical biomes to move poleward—towards the north pole in the northern hemisphere and towards the south pole in the southern hemisphere (Carter et al., 2018; Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Day et al., 2013; Parmesan, 2006; Yamano, Sugihara, & Nomura, 2011). Scientists have used the term “tropicalization” to describe the transformation of temperate ecosystems by these poleward-moving tropical species (Macy et al., 2019; Osland & Feher, 2020; Scheffell, Heck, & Johnson, 2018; Vergés et al., 2014; Yáñez-Arancibia, Day, Twilley, & Day, 2014). In coastal wetland ecosystems, warming winter air temperatures are expected to allow tropical mangrove forests to move poleward, in some cases at the expense of temperate salt marsh ecosystems (Cavanaugh et al., 2019; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). The ecological implications of these marsh-to-mangrove transformations are large (Guo et al., 2017; Kelleway et al., 2017), and ecologists working near mangrove range limits are increasingly challenged to better understand the drivers and implications of mangrove range expansion. Here, we investigated the influence of winter air temperature regimes on the distribution and structure of mangroves near a northern range limit in wetland-rich Louisiana (USA).

At global and regional scales, winter temperatures govern the distribution (Cavanaugh et al., 2018; Osland, Feher, et al., 2017; Woodroffe & Grindrod, 1991), abundance (Osland, Day, et al., 2017; Ross, Ruiz, Sah, & Hanan, 2009), height (Feher et al., 2017; Gabler et al., 2017; Rovai et al., 2016; Simard et al., 2019; Simpson, Osborne, Duckett, & Feller, 2017), diversity (Chen et al., 2017; Ellison, 2002; Morrissey et al., 2010; Osland, Feher, et al., 2017), productivity (Bouillon et al., 2008; Cavanaugh et al., 2014; Feher et al., 2017; Ribeiro, Rovai, Twilley, & Castañeda-Moya, 2019), reproduction (Dangremond & Feller, 2016; Duke, 1990; Hong et al., 2020) and physiology (Lovelock, Krauss, Osland, Reef, & Ball, 2016; Stuart, Choat, Martin, Holbrook, & Ball, 2007) of mangrove forests. However, the influence of winter temperature regimes varies greatly within and across range limits (Cavanaugh et al., 2018; Cook-Patton, Lehmann, & Parker, 2015; Osland, Feher, et al., 2017; Quisthoudt et al., 2012). While some range limits (e.g., eastern North America) are controlled by extreme freeze events (e.g., individual freeze events that may occur for just a few days once every decade or two), others are controlled by consistently cold temperatures that

are slightly above freezing for the entire winter (e.g., Australia, South Africa, South America, New Zealand; Cavanaugh et al., 2018; Morrissey et al., 2010; Osland, Feher, et al., 2017; Stuart et al., 2007).

Coastal wetland scientists working in eastern North America have long recognized that the frequency of extreme freeze events governs the northern range limits of mangrove forests in Texas, Louisiana and Florida (Kennedy, Preziosi, Rowntree, & Feller, 2020; Lloyd & Tracy, 1901; Lonard & Judd, 1991; Lugo & Patterson-Zucca, 1977; Sherrod & McMillan, 1985; West, 1977). However, extreme freeze events that lead to mangrove mortality or damage are infrequent and difficult to study (Osland, Day, et al., 2020; Pickens, Sloey, & Hester, 2019; Ross et al., 2009). Moreover, mangrove distribution data have historically been lacking near northern range limits in this region (Armitage, Highfield, Brody, & Louchouart, 2015; Giri & Long, 2014, 2016; Osland et al., 2018). Thus, the influence of extreme freeze events on mangrove distribution and structure has been poorly quantified.

There are three common mangrove species in North America: *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* (Tomlinson, 1986). Of these three species, *A. germinans* (black mangrove) is the species that is most freeze-tolerant and the species whose distribution extends farthest north in eastern North America. To our knowledge, *A. germinans* is the only mangrove species that is currently present in Louisiana. In this study, we investigated the following questions for the northern range limit of *A. germinans* in Louisiana: (1) Within the past 30 years (i.e., 1989–2018), what has been the frequency and spatial distribution of extreme freeze events with the potential to cause *A. germinans* mortality and/or leaf damage? (2) Where is *A. germinans* located and how is its distribution influenced by the spatial distribution of extreme freeze events? (3) What are the relationships between the frequency of extreme freeze events and the abundance, height and coverage of *A. germinans*? and (4) How does the risk of *A. germinans* freeze damage vary spatially across coastal Louisiana? Advancing knowledge on these topics will help scientists and natural resource managers better anticipate and prepare for the tropicalization of coastal wetlands due to climate change.

## 2 | METHODS

### 2.1 | Study area background: coastal Louisiana

Coastal Louisiana is positioned within the dynamic Mississippi River Delta, which is one of the largest river deltas in the world. In addition to providing valuable fish and wildlife habitat, Louisiana's abundant wetlands offer protection from storms, improve water quality, sequester carbon from the atmosphere, support food

webs, provide seafood, store floodwaters and provide recreational opportunities (Barbier et al., 2011; Costanza et al., 2014). Though difficult to quantify, the societal benefits (i.e., ecosystem services) provided by coastal ecosystems in Louisiana's Mississippi River Delta have been valued to be at least \$12–\$47 billion (US dollars) per year (Batker et al., 2010). However, the rate of wetland loss in Louisiana has been very high in the past century, due to a combination of natural and human factors that have reduced the ability of wetlands to build elevation to keep pace with high rates of subsidence and relative sea-level rise (Blum & Roberts, 2009; Day et al., 2007; Törnqvist, Jankowski, Li, & González, 2020). Between 1932 and 2016, Louisiana lost approximately 4,833 km<sup>2</sup> of wetlands (Couvillion, Beck, Schoolmaster, & Fischer, 2017), and the state has become a prominent global example of the negative linkages between high relative sea-level rise, sediment delivery alterations and coastal wetland loss (Jankowski, Törnqvist, & Fernandes, 2017; Twilley et al., 2016). Given the rapid pace of wetland loss in the last century and the expectation of accelerated sea-level rise in the coming century, coastal scientists in Louisiana are increasingly challenged to better anticipate and prepare for the effects of climate change on Louisiana's coastal wetlands (Coastal Protection & Restoration Authority of Louisiana, 2017). However, Louisiana's coastal wetlands are vulnerable to interactions between many different aspects of climate change. For example, accelerated sea-level rise, intensifying hurricanes, more extreme drought, more extreme precipitation and winter warming are all aspects of climate change that are projected to play increasingly important roles in Louisiana (Carter et al., 2018; USGCRP, 2017, 2018).

Winter warming is a critical component of climate change that is expected to transform Louisiana's coastal ecosystems (Gabler et al., 2017; Osland, Day, et al., 2017; Osland, Enwright, Day, & Doyle, 2013). Extreme freeze events have historically served as major ecological disturbances in Louisiana and other tropical–temperate transition zones across North America—leading to mass mortality of freeze-sensitive organisms. Freeze events control the distribution of mangrove forests in Louisiana (Osland, Day, et al., 2017) and across the northern Gulf of Mexico and Atlantic coasts of North America (Cavanaugh et al., 2014; Osland et al., 2013; Ross et al., 2009; Sherrod & McMillan, 1985; Stevens, Fox, & Montague, 2006). Most of Louisiana's salt-affected tidal wetlands (i.e., those in the saline, brackish and intermediate salinity classes) are currently dominated by freeze-tolerant salt marsh graminoid plants (i.e., grasses, sedges and rushes; Osland, Grace, et al., 2019; Sasser, Visser, Mouton, Linscombe, & Hartley, 2014; Visser, Sasser, Chabreck, & Linscombe, 1998, 2000). Due to their current and historical role as critical foundation plant species (*sensu* Ellison, 2019; Ellison et al., 2005), these graminoid-dominated salt marsh plant communities tend to be the target of future-focused ecological assessments and restoration-focused planning efforts for coastal Louisiana (Coastal Protection & Restoration Authority of Louisiana, 2017). However, the outer coast of Louisiana contains a dynamic and climate-sensitive mangrove–marsh ecotone that has the potential to

be transformed by warming winters (Gabler et al., 2017; Osland et al., 2013).

How long have mangroves been present in Louisiana? The recent ~30-year expansion of mangroves since the last major, mortality-inducing freeze event in 1989 happens to coincide with the availability of remotely sensed Landsat data; thus, there has been some debate regarding the novelty of the last 30 years of mangrove expansion in eastern North America (Armitage et al., 2015; Cavanaugh et al., 2014, 2019; Giri & Long, 2014, 2016; Osland, Day, et al., 2017; Saintilan et al., 2014). Historical literature accounts show that *A. germinans* has been present and documented in Louisiana for at least 300 years—dating back to the period of active European exploration and colonization (Table 1). One of the first Europeans to write about Louisiana plants was Antoine-Simon Le Page du Pratz (Ewan, 2005), a Dutch, engineer, historian and naturalist that lived in Louisiana between 1718 and 1734. Le Page du Pratz (1774) wrote that “the mangrove is common all over America. It grows in Louisiana near the sea, even to the bounds of low water mark.” Dutch surveyor Bernard Romans noted the presence of mangroves on the Chandeleur Islands in 1772 (Romans, 1775). In 1779, French surveyor Jean Francois Gonsoulin described mangroves near Cat Island Pass during an effort to find a coastal navigation route between New Iberia and New Orleans (Weddle, 1995). Based upon their travels in the south-eastern United States in the late 1700s, French botanists André Michaux and son Francois André Michaux wrote that *A. germinans* “extends from Texas to Florida” and was present in Louisiana near the mouth of the Mississippi estuary and New Orleans (Michaux & Nuttall, 1859). In 1812, English botanist Thomas Nuttall collected an herbarium specimen of *A. germinans* from an undisclosed location south of New Orleans (<http://plants.jstor.org/stable/10.5555/al.ap.specimen.ph00005841>). In a 1901 description of the vegetation on Louisiana's barrier islands, botanists Frank Lloyd and Samuel Tracy indicate that freeze-stunted *A. germinans* were common in certain areas and especially on Breton Island. Tulane botanist Reginald Cocks collected an herbarium specimen of *A. germinans* near Grand Island in 1908 (<https://s3.amazonaws.com/huhspecimenimages/JPG-Preview/01799838.jpg>), noting that it was “very abundant.” In an article on Louisiana trees (1921), Cocks wrote that *A. germinans* is present “along the seacoast and adjacent islands, forming occasionally dense thickets. Occasionally a tree 30 feet high.” A video taken in 1915 on a Louisiana barrier island near or within Breton National Wildlife Refuge shows former president Theodore Roosevelt standing within dense *A. germinans* stands (<https://www.loc.gov/item/mp76000363>). There are many more observations in early 20th century literature of *A. germinans* presence in Louisiana (e.g., Bent, 1910; Brown, 1930; Kopman, 1915; Moore, 1899; Penfound & Hathaway, 1938), and digital herbarium records of *Avicennia* in Louisiana, available on the Southeast Regional Network of Expertise and Collections (<http://sernecportal.org>), show that *A. germinans* has been collected throughout much of the last century in the following south-eastern Louisiana parishes (listed in descending rank order by number of records in parentheses): Lafourche (44), Jefferson (30), Terrebonne (18), St. Bernard (9) and Plaquemines (8). An historical

Observation year(s)	Individual	Type	Source
1718–1734	Antoine-Simon Le Page du Pratz	Literature	Le Page du Pratz (1774), Arthur (1947)
1772	Bernard Romans	Literature	Romans (1775)
1779	Jean Francois Gonsoulin	Literature	Weddle (1995)
Late 1700s	André Michaux and Francois André Michaux	Literature	Michaux and Nuttall (1859)
1812	Thomas Nuttall	Herbarium	Academy of Natural Sciences Herbarium
1897–1898	Henry Moore	Literature	Moore (1899)
1900	Frank Lloyd and Samuel Tracy	Literature	Lloyd and Tracy (1901)
1907	Henry Kopman	Literature	Kopman, 1915
1908	Reginel Cocks	Herbarium	Harvard Herbarium
Early 1900s	Reginel Cocks	Literature	Cocks (1921)
1910	Arthur Bent	Literature	Bent (1910)
1913	Edwin Wurzlow	Herbarium	LSU Herbarium
1915	Theodore Roosevelt	Video	Library of Congress video
1928	Clair Brown	Literature	Brown (1930)
1931	Lulu Cangemi and Lucille Andrus	Herbarium	LSU Herbarium
1932–1933	William Penfound and Edward Hathaway	Literature	Penfound and Hathaway (1938)
1948	Joseph Ewan	Herbarium	Duke Herbarium

Note: The records shown are those found before 1950. Multiple records were also found for the 1950s and 1960s, and nearly continuous records (i.e., annual or biennial accounts) are available between 1970 and 2020.

**TABLE 1** Historical literature accounts and herbarium records show that *A. germinans* has been present along the south-eastern outer coast of Louisiana for at least 300 years—dating back to the period of active European exploration and colonization

analysis of records from a similar mangrove range limit along the Atlantic coast of Florida indicates that mangroves have also been present there for at least several centuries—Cavanaugh et al. (2019) identified reports of mangrove presence in north-eastern Florida dating back to 1766 and 1788 by botanists William Bartram (Bartram & Harper, 1943) and André Michaux (Michaux & Sargent, 1889), respectively.

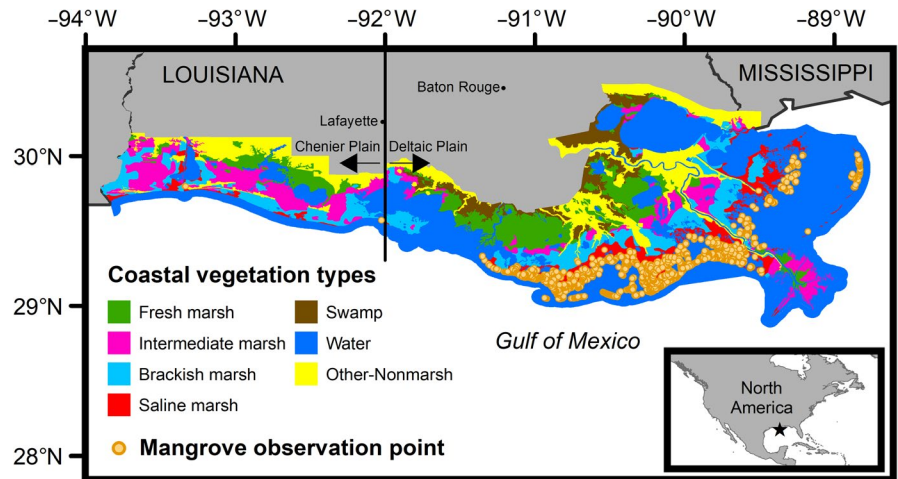
An analysis that used historical temperature records dating back to 1890s and mangrove abundance data near Port Fourchon dating back to the 1970s indicates that the mangrove range limit in Louisiana has expanded and contracted many times in response to the absence or presence of winter temperature extremes, respectively (Osland, Day, et al., 2017). During warm periods, freeze-sensitive mangroves have expanded as they outcompete salt marsh graminoids. Conversely, following extreme freeze events that kill or damage mangroves, the coverage of freeze-tolerant salt marshes has expanded. Similar mangrove expansion and contraction cycles have also occurred in Florida (Cavanaugh et al., 2019; Stevens et al., 2006) and other mangrove range limits across eastern North America (Kennedy et al., 2016, 2017; Sherrod & McMillan, 1981, 1985). Since the last regionally relevant major freeze event occurred in December 1989, the mangrove-marsh ecotone has been expanding northward

in Louisiana and across the region (e.g., in coastal Texas and both coasts of the Florida peninsula). Mangrove range limits in the region are expected to continue to expand farther north in response to warming winters (Osland et al., 2018). In the face of climate change, mangroves are increasingly seen as potential vegetation targets for coastal wetland restoration and planning efforts (Hijuelos et al., 2019; Mack et al., 2014; USDA-NRCS, 2017). For example, mangrove seedlings are sometimes planted at restoration sites, and mangrove propagules have also been occasionally collected and dispersed into salt marshes. Mangroves may also be a target vegetation that would establish within planted marsh vegetation following natural recruitment of mangrove propagules from adjacent mangrove stands. However, to better inform restoration practices, there is a need to better understand the influence of extreme freeze events upon mangrove distribution and structure near this range limit.

## 2.2 | Study grid creation

Our study area included all of coastal Louisiana (Figure 1), which can be coarsely divided into two geomorphic regions: the Mississippi River Deltaic Plain (Bahr et al., 1983) to the east and the Chenier

**FIGURE 1** Map of *Avicennia germinans* (black mangrove) distribution in Louisiana (USA). Each of the orange circles represents a mangrove observation point recorded via aerial surveys from a fixed-wing aircraft in 2009 (Day et al., 2020; Michot et al., 2010). The seven coastal vegetation types are from Sasser et al. (2014). Winter air temperature extremes (i.e., freeze events) constrain Louisiana mangroves primarily to saline and brackish marshes of the south-eastern outer coast



Plain (Gosselink, Cordes, & Parsons, 1979) to the west (Bentley, Blum, Maloney, Pond, & Paulsell, 2016; Blum & Roberts, 2012; Gould & McFarlan, 1959; Jankowski et al., 2017). Within the study area, we created a grid of cells (hereafter, the study grid) for quantifying the frequency of freeze events and depicting the risk of mangrove freeze damage and mortality. The study grid was created using the registration of the gridded climate data used in this study (i.e., 2.5-arcmin [ $\sim 4$  km] minimum air temperature data created by the PRISM Climate Group, Oregon State University [prism.oregonstate.edu]).

### 2.3 | Mangrove data

We incorporated *A. germinans* abundance, height and cover data for the year 2009 from a U.S. Geological Survey Data Release (Day, Michot, Twilley, & From, 2020). To characterize the distribution of *A. germinans* across coastal Louisiana, Richard H. Day and Thomas C. Michot conducted aerial surveys from a fixed-wing aircraft between January and April 2009 (Day et al., 2020; Michot, Day, & Wells, 2010). Their surveys identified 4,382 mangrove observation points, which each span a  $\sim 7,854$  m<sup>2</sup> circular area (i.e., a 100 m diameter circle). For each observation point, the centre coordinates were recorded, and the observation point was placed into one of two mangrove height categories and one of three mangrove cover categories. The two mangrove height categories included the following: (1) short mangroves [i.e., height < 2 m]; and (2) tall mangroves [i.e., height > 2 m]. The three mangrove cover categories included the following: (1) one to many scattered individuals not touching each other; (2) linear groupings of adjacent plants; and (3) solid masses of adjacent plants covering all or part of the observation area (i.e.,  $\sim 7,854$  m<sup>2</sup>). This mapping effort produced a snapshot of the entire geographical distribution of *A. germinans* in coastal Louisiana during the spring of 2009 but did not estimate areal coverage.

### 2.4 | Station-based temperature data

Our final freeze frequency analyses relied on gridded temperature data; however, we used station-based daily minimum temperature

data to identify freeze events for which gridded data were obtained and analysed in more detail. Station-based data were obtained from the United States Historical Climatology Network (USHCN) for a station in Lafayette, Louisiana (Lafayette Regional Airport; Station ID: GHCND: USW00013976). We obtained daily minimum temperature data for the 30-year period extending from 1 January 1989 to 31 December 2018. We identified 19 days within this 30-year period that had minimum temperatures less than  $-6^{\circ}\text{C}$  at this inland station. During freeze events, air temperatures are approximately  $2.2^{\circ}\text{C}$  warmer along the coast, where mangrove forests are present, compared to inland (Osland, Day, et al., 2017). Thus, using this temperature cut-off for an inland location (i.e., Lafayette) provided us with a conservative dataset for quantifying the frequency of events with the potential to lead to mangrove mortality or damage along the slightly warmer coast, where temperatures during these events should fall below approximately  $-3.8^{\circ}\text{C}$ . *Avicennia germinans* leaf damage in this area typically begins at temperature less than  $-4.2^{\circ}\text{C}$  (Osland, Day, et al., 2020).

### 2.5 | Gridded temperature data

For each of the 19 days that were identified as having potentially ecologically relevant minimum temperatures, we obtained continuous gridded daily minimum air temperature data that were created by the PRISM Climate Group using the PRISM (Parameter-elevation Relationship on Independent Slopes Model) interpolation method (Daly et al., 2008). The PRISM data were selected because the PRISM model accounts for land-ocean temperature gradients (Daly et al., 2008; Daly, Helmer, & Quiñones, 2003; Daly, Widrechner, Halbleib, Smith, & Gibson, 2012) that influence spatial patterns of mangrove mortality and damage (Osland, Day, et al., 2017, 2020).

### 2.6 | Data analyses: freeze frequency

We defined potential mangrove mortality and leaf damage events as freeze events with temperatures below  $-6.6^{\circ}\text{C}$  and between



−4.2°C and −6.6°C, respectively (Osland, Day, et al., 2020). For each cell within the study grid and for each mangrove observation point, we used the daily gridded climate data to determine the number of events (i.e., the frequency of extreme freeze events) that would lead to mangrove mortality or leaf damage during 30-year (1989–2018), 20-year (1999–2018) and 10-year periods (2009–2018).

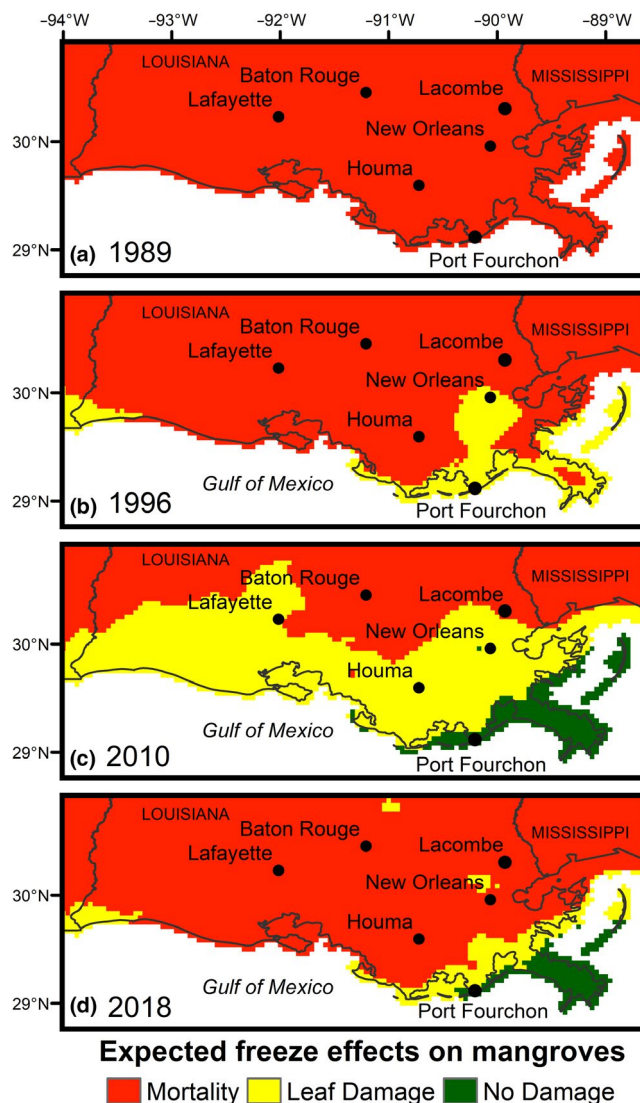
## 2.7 | Data analyses: freeze–mangrove relationships and spatial depictions of mangrove risk

We used regression analyses to quantify the relationships between two temperature-based variables (i.e., the 30-year frequency of freeze mortality events and leaf damage events) and the number of mangrove observations point in the following: (a) all categories; (b) the tall category; and (c) the solid cover category. For each analysis, we compared linear and exponential decay models. A linear equation was selected for one regression model (i.e., the relationships between leaf damage event frequency and number of mangrove observation point in all categories). Exponential decay equations were selected for the other five regression models. For four of the most severe freeze events (22–25 December 1989, 3–5 February 1996, 9–11 January 2010, and 17–18 January 2018), we used the mangrove mortality and damage thresholds to produce maps that spatially depict the expected freeze effects in three categories: (a) mortality [i.e., temperatures < −6.6°C], (b) leaf damage [i.e., temperatures between −4.2°C and −6.6°C] and (c) no damage [i.e., temperatures above −4.2°C]. We also produced maps that spatially depict the number of events (i.e., frequency) that would lead to mangrove mortality or leaf damage during 30-year (1989–2018), 20-year (1999–2018) and 10-year periods (2009–2018). Finally, we produced maps depicting the risk of mangrove freeze damage using the 30-year frequency of mangrove damage events. Moderate, high and very high categories for risk of mangrove freeze damage were assigned to areas that were determined to have 2 to 3, 4 to 5, and ≥6 potential leaf damage events during the 30-year period, respectively. All spatial analyses were conducted using ArcGIS 10.6 (Environmental Systems Research Institute, Inc.). All regression analyses were conducted in SigmaPlot 12.5 (Systat software, Inc.).

## 3 | RESULTS

### 3.1 | Severe freeze events between 1989 and 2018

For the 30-year period between 1989 and 2018, our analyses identified 11 events with the potential to cause mangrove damage or mortality somewhere in coastal Louisiana. In Figure 2, we highlight four of the most severe freeze events: 22–25 December 1989 (Figure 2a), 3–5 February 1996 (Figure 2b), 9–11 January 2010 (Figure 2c) and 17–18 January 2018 (Figure 2d). The other seven freeze events identified include the following: 16 December 1989, 19 December 1996, 4 January 2002, 24 January 2003, 13 January 2011, 7 January



**FIGURE 2** The temperature-based potential for *Avicennia germinans* (black mangrove) mortality and leaf damage in Louisiana during four different freeze events: (a) 22–25 December 1989, (b) 3–5 February 1996, (c) 9–11 January 2010 and (d) 17–18 January 2018. Potential mortality and leaf damage events were defined as freeze events with temperatures below −6.6°C and between −4.2°C and −6.6°C, respectively (Osland, Day, et al., 2020). Note that these maps represent events with the potential to affect mangroves regardless of whether they are present. See Figure 1 for current mangrove distribution

2014 and 30 January 2014. The 1989 Christmas freeze (i.e., 22–25 December) was the most severe with temperatures cold enough to cause mangrove mortality across all of Louisiana (note red in Figure 2a). During the 1989 Christmas freeze, minimum temperatures near coastal Port Fourchon and inland Lacombe were estimated to be −9 and −12°C, respectively, which are far below the −6.6°C threshold for mangrove mortality. Note that mangroves are present near the warmer, coastal Port Fourchon but not in the salt marshes near the colder, inland Lacombe. These two locations are provided to show the contrast in temperatures between inland and coastal Louisiana during extreme freeze events. During the 1996,

2010 and 2018 events, the temperatures were much less severe than the 1989 Christmas freeze but cold enough to result in some mangrove mortality and leaf damage in certain areas (note red and yellow areas in Figure 2b–d, respectively). Near coastal Port Fourchon, the minimum temperatures during the 1996, 2010 and 2018 events were estimated to be  $-5$ ,  $-3$  and  $-4^{\circ}\text{C}$ , respectively. Near inland Lacombe, the minimum temperatures for these three events were estimated to be  $-8$ ,  $-7$  and  $-8^{\circ}\text{C}$ , respectively.

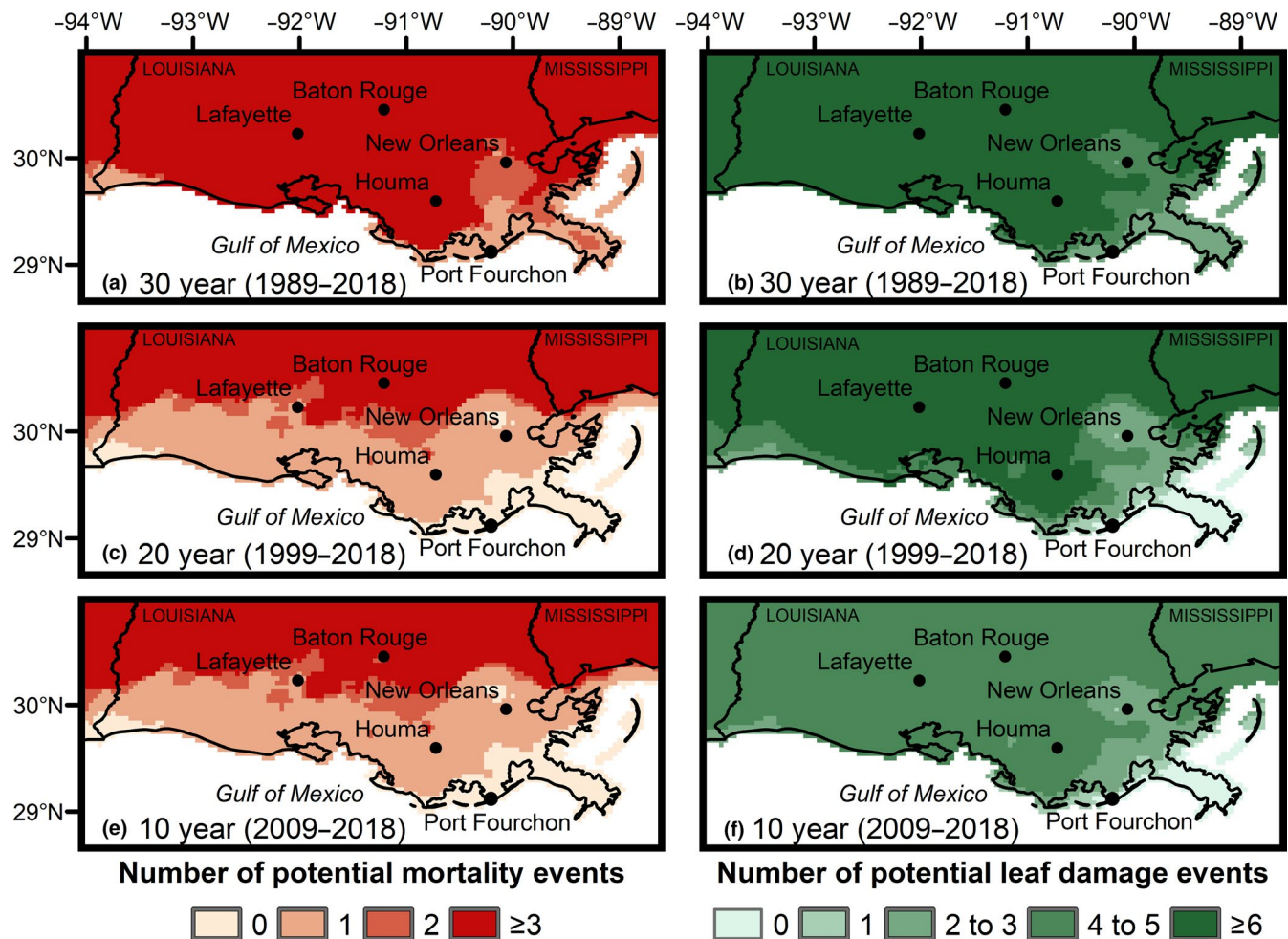
### 3.2 | Frequency of extreme freeze events

We used the gridded temperature data to produce maps of the frequency of freeze events with the potential to cause mangrove mortality and mangrove leaf damage in Louisiana across 30-year (Figure 3a,b), 20-year (Figure 3c,d) and 10-year periods (Figure 3e,f). These maps corroborate the hypothesis that temperatures are colder in the Chenier Plain (compared to the Deltaic Plain) and in

inland Louisiana (compared to coastal Louisiana). Note that the mangrove observation points shown in Figure 1 are in areas where the frequency of extreme freeze events is lowest (i.e., the south-eastern outer coast).

### 3.3 | Mangrove abundance, height, and cover and the influence of freeze frequency

The aerial surveys identified 4,382 mangrove observation points, which were mostly located along the south-eastern outer coast in areas that are classified as saline or brackish marshes in Sasser et al. (2014) (Figure 1). The potential for freeze-induced mangrove mortality is higher along the Chenier Plain compared to the outer coast of the Deltaic Plain (Figures 2 and 3). Thus, in 2009, only four mangrove observation points were identified in the Chenier Plain (Figure 1)—these were observed on Marsh Island (one plant in the short height category) and Monkey Island (one and two plants in the tall and short



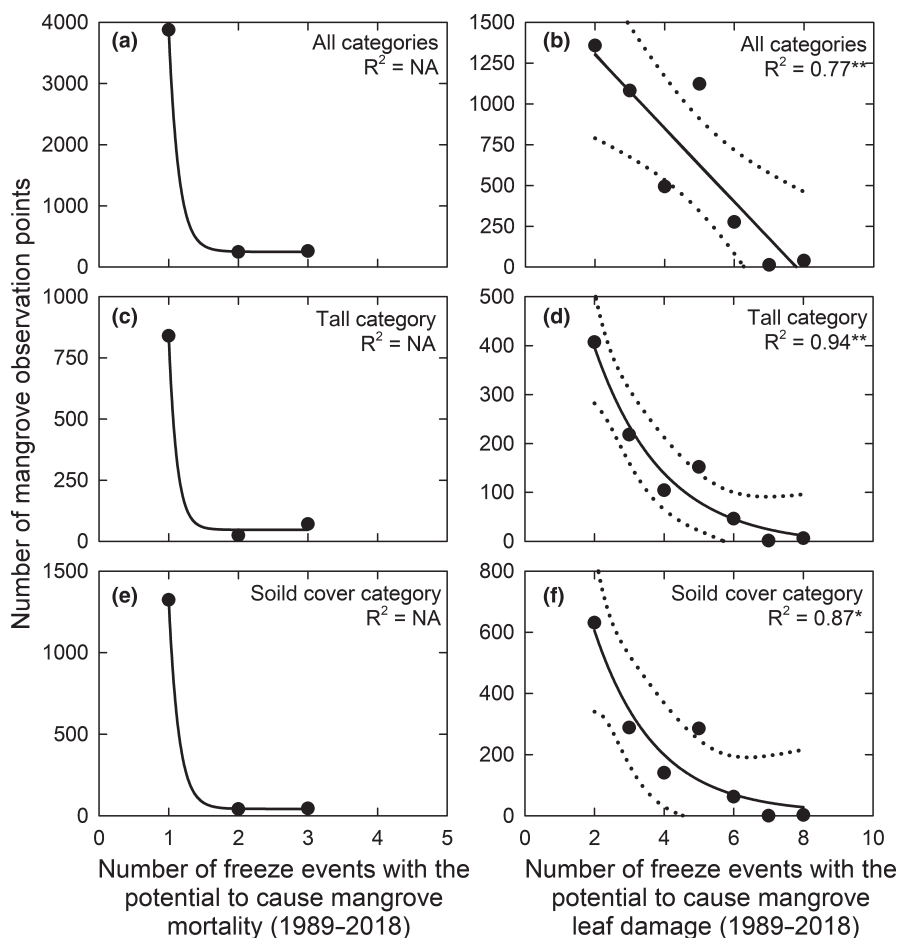
**FIGURE 3** The frequency of freeze events with the potential to cause mangrove mortality (left panels) and mangrove leaf damage (right panels) in Louisiana. Frequency was quantified across 30-year (a, b), 20-year (c, d) and 10-year periods (e, f). These three periods include freeze events that occurred between 1989 and 2018, 1999 and 2018, and 2009 and 2018, respectively. Potential mortality and leaf damage events were defined as freeze events with temperatures below  $-6.6^{\circ}\text{C}$  and between  $-4.2^{\circ}\text{C}$  and  $-6.6^{\circ}\text{C}$ , respectively (Osland, Day, et al., 2020). Note that these maps represent events with the potential to affect mangroves regardless of whether they are present. See Figure 1 for mangrove distribution in 2009

height categories, respectively; Day et al., 2020; Michot et al., 2010). The potential for freeze-induced mangrove mortality is higher in inland areas compared to the outer coast (Figures 2 and 3). Thus, in 2009, almost all the observation points (4,378 out of 4,382 = 99.91%) were identified in the Deltaic Plain within the outer coastal areas of the Barataria, Terrebonne, Breton Sound and Pontchartrain Basins (i.e., Lafourche, Jefferson, Terrebonne, St. Bernard and Plaquemines Parishes). Mangroves are particularly abundant in areas surrounding Port Fourchon. Other mangrove distribution hotspots include areas near Bay Junop, Caillou Bay, Isle Dernières, Timbalier Island, Grand Isle, Bay Melville, Bay Long and the Chandeleur Islands. In terms of tree height, 3,448 and 934 observation points were in the short (<2 m) and tall (>2 m) categories, respectively. In terms of cover, 1,855 observation points included one to many scattered individuals, 1,119 observation points included linear groupings of adjacent plants, and 1,408 observation points contained solid masses of adjacent plants covering all or part of the ~7,854 m<sup>2</sup> observation areas. Solid masses of tall plants were clustered closer to the coast, while short individual plants were more numerous away from the coast within interior wetlands. We quantified strong negative relationships between the 30-year frequency of freeze mortality events and leaf damage events and *A. germinans* abundance (Figure 4a,b), height (Figure 4c,d) and coverage (Figure 4e,f), respectively. We used this information along with our spatial analyses of freeze frequency to produce maps of the risk of mangrove freeze damage (Figure 5a,b).

## 4 | DISCUSSION

Of the three south-eastern U.S. states with expanding mangrove range limits (i.e., Florida, Louisiana and Texas), Florida is the state with the largest mangrove coverage (Giri & Long, 2016; Osland et al., 2018) and the only state with reliable statewide mangrove areal coverage data (Florida Department of Transportation, 1999; Kawula & Redner, 2018). In the past decade, several studies have used mangrove coverage data from Florida to advance understanding of the influence of freeze events on mangrove distribution near range limits along Florida's Gulf of Mexico and Atlantic coasts (e.g., Cavanaugh et al., 2019, 2014; Osland et al., 2013). In contrast, the lack of statewide mangrove areal coverage data in Texas and Louisiana has constrained advances in knowledge regarding the influence of freeze events on mangrove range expansion in those states. Ecologists working in Louisiana's mangrove-marsh ecotone have long recognized the importance of extreme freeze events (Lloyd & Tracy, 1901; McKee & Vervaeke, 2018; Michot et al., 2010; West, 1977), but data limitations have meant that research on this topic in Louisiana has been constrained to isolated observations of mangrove freeze damage or local studies focused on the effects of specific freeze events (Osland et al., 2015; Osland, Day, et al., 2017, 2020; Pickens et al., 2019).

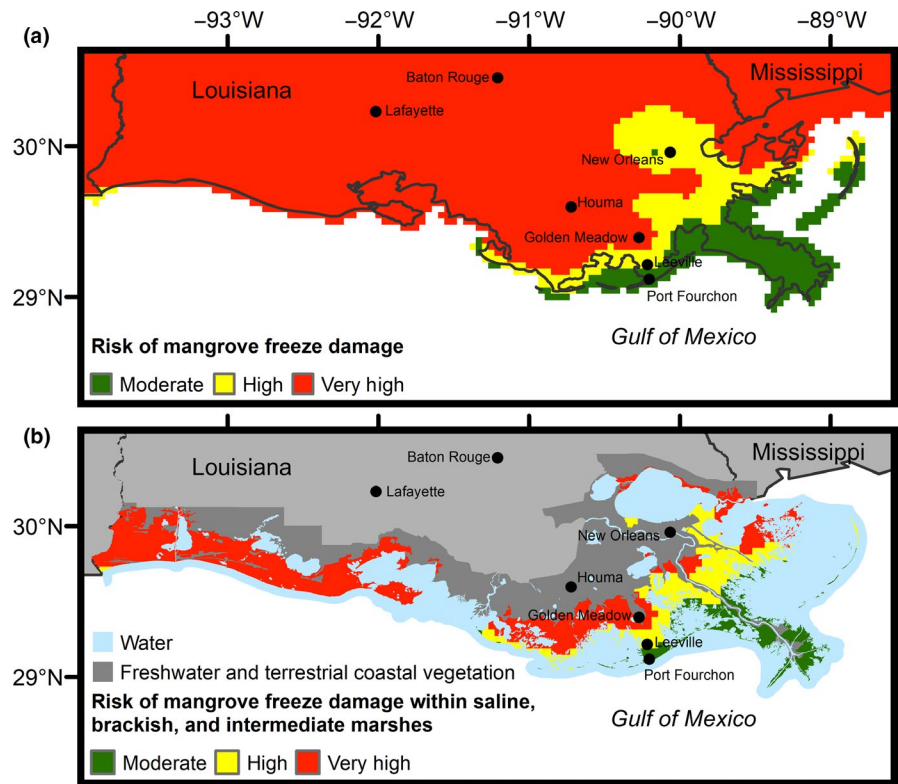
For the *A. germinans* range limit in Louisiana, our findings quantify the influence of the frequency of extreme freeze events upon



**FIGURE 4** The relationships between the frequency of freeze events and the number of mangrove observation points in the following: (a, b) all mangrove categories; (c, d) the tall mangrove category (i.e., height greater than 2 m); and (e, f) the solid mangrove cover category (i.e., groups of several plants up to continuous mangrove cover in areas up to 7,850 m<sup>2</sup>). The mangrove observation points were recorded via aerial surveys from a fixed-wing aircraft in 2009 (Day et al., 2020; Michot et al., 2010). The x axes represent the number of freeze events with the potential to cause mangrove mortality (left panels) or leaf damage (right panels) across a 30-year period (1989–2018)



**FIGURE 5** Maps of the risk of mangrove freeze damage in Louisiana. Risks levels were assigned based upon the frequency of freeze events cold enough to lead to mangrove leaf damage between 1989 and 2018. Based solely upon winter air temperature regimes, mangrove establishment and growth are most likely to be successful within the moderate freeze damage risk zone identified in green. The risk of mangrove freeze damage is high and very high within the yellow and red zones, respectively. While the upper map (a) displays continuous zones across all coastal vegetation categories, the lower map (b) displays mangrove freeze damage risk within just the saline, brackish and intermediate marsh categories, which are the salinity regimes most likely to support mangroves



mangrove distribution, height and coverage. *Avicennia germinans* is most abundant, tall and continuous along the south-eastern outer coast of Louisiana's Mississippi River Deltaic Plain, where the risk of mangrove freeze damage and/or mortality is reduced due to the buffering effects of large expanses of comparatively warmer water and saturated wetland soils, which produce ecologically relevant land-ocean temperature gradients (Osland, Day, et al., 2017; Osland, Hartmann, et al., 2019). In contrast, mangroves have historically been absent or less abundant along the Chenier Plain and in the inner sections of the Deltaic Plain due primarily to the higher frequency of extreme freeze events in those areas. Stated more concisely, due to spatial variability in the frequency of extreme freeze events, the risk of mangrove freeze damage in Louisiana is highest along the Chenier Plain and interior Deltaic Plain and lowest along the south-eastern outer coast of the warmer Deltaic Plain (Figure 5). Observations in the literature have also noted the influence of similar land-ocean temperature gradients on mangrove distribution patterns in Texas (Sherrod & McMillan, 1981, 1985) and Florida (Davis, 1940; Olmsted, Dunevitz, & Platt, 1993; Stevens et al., 2006). Literature observations (Table 1), herbarium records (Table 1), historical landscape-level plant surveys (e.g., Chabreck, 1970; Visser et al., 1998; Visser et al., 2000), and Coastwide Reference and Monitoring System (CRMS) network vegetation data (<https://lacoast.gov/crms>) all support this finding as mangroves have historically been observed and collected primarily along the outer coast of south-eastern Louisiana (i.e., along the outer coasts of Lafourche, Jefferson, Terrebonne, St. Bernard and Plaquemines parishes). To our knowledge, only one herbarium record has been

collected from the Chenier Plain—on Monkey Island in Cameron Parish by W.G. Vermillion in 2002. In this study, mangroves were also observed in Iberia Parish on Marsh Island.

#### 4.1 | Coastal restoration implications

Due to the rapid pace of coastal wetland loss in Louisiana, wetland restoration is a high priority (Coastal Protection & Restoration Authority of Louisiana, 2017). Historically, wetland restoration efforts in Louisiana have targeted plant communities dominated by marsh grasses, sedges or rushes. However, due to the recent increases in *A. germinans* abundance and height since the last major freeze event in 1989, mangrove-dominated plant communities are increasingly viewed as potential vegetation targets for tidal saline and/or brackish wetland restoration efforts (Hijuelos et al., 2019; Mack et al., 2014; USDA-NRCS, 2017). Our findings provide the first state-level maps of the risk of mangrove freeze damage in Louisiana. These maps can be used to identify the following: (a) areas where *A. germinans* planting or propagule release during wetland restoration may be risky due to a very high or high risk of mangrove freeze damage (see red and yellow areas in Figure 5b, respectively); and (b) areas where *A. germinans* could potentially be targeted during wetland restoration due to a moderate risk of mangrove freeze damage (see green areas in Figure 5b). However, note that our results indicate that there is at least a moderate risk of mangrove freeze damage across the entire state. Although the resistance and resilience of *A. germinans* to freezing has likely increased in the last 30 years (Osland et al.,

2015; Osland, Hartmann, et al., 2019), a major freeze event like those that occurred in the 1980s would have the potential to damage mangroves across the entire Louisiana coast (e.g., see red in Figure 2a for the 1989 Christmas freeze). Freeze events that result in massive mangrove mortality also have the potential to result in peat collapse, erosion and conversion of coastal wetlands to open water if post-disturbance natural regeneration does not occur quickly (Cahoon et al., 2003; Chambers, Steinmuller, & Breithaupt, 2019; Osland, Feher, Anderson, et al., 2020; Ward, Friess, Day, & MacKenzie, 2016). For example, on the Timbalier and Isle Dernières barrier island arcs, mangrove dieback during extreme freeze events in the 1980s are thought to have contributed to more rapid rates of erosion and shoreline change (McBride & Byrnes, 1997; Penland et al., 2003). Thus, given the potential for adverse effects due to freezing, caution is advised when targeting *A. germinans*-dominated plant communities during wetland restoration in Louisiana. Although the frequency and intensity of extreme freeze events are expected to decrease by the end of the century, there is some debate regarding the potential for extreme freeze events in the coming decades. Much of the debate centres on linkages between rapid Arctic warming (i.e., Arctic amplification) and jet stream dynamics that affect midlatitude climates, including the frequency and intensity of extreme freeze events in the near term (Cohen, Pfeiffer, & Francis, 2018; Cohen et al., 2019; Dai & Song, 2020; Zhang, Tian, Chipperfield, Xie, & Huang, 2016).

In addition to the risk that planted seedlings will be killed by extreme freezing temperatures, there is increasing evidence that salt marsh grasses (e.g., *Spartina alterniflora*) are able to more effectively jump-start coastal wetland restoration efforts compared to mangroves due to the more rapid growth, horizontal expansion and recruitment of marsh grasses compared to mangroves (specifically, *A. germinans*; Yando, 2018; Yando, Osland, Jones, & Hester, 2019). Once established, planted salt marsh grasses can help trap mangrove propagules and facilitate the natural recruitment and growth of *A. germinans* seedlings (Donnelly, Walters, & coasts, 2014; Osland, Feher, Spivak, et al., 2020; Peterson & Bell, 2012). In physiologically challenging environments, herbaceous marsh plants have the potential to function as nurse plants that ameliorate stressful edaphic physicochemical conditions and accelerate mangrove forest development (McKee, Rooth, & Feller, 2007). Marsh plants can even provide microclimatic conditions that protect mangrove seedlings from moderate freeze events (Coldren & Proffitt, 2017; Devaney, Lehmann, Feller, & Parker, 2017; Osland, Hartmann, et al., 2019). In areas where mangrove propagules are abundant, planting mangroves is often not necessary because mangroves can typically recruit naturally into a restoration site once the appropriate hydrologic regime has been established. So, instead of directly planting mangroves, many mangrove restoration efforts plant salt marsh grasses, which, in addition to being freeze tolerant, can more quickly stabilize substrates and provide plant coverage that facilitates natural mangrove recruitment (Lewis, 2009; Lewis & Dunstan, 1975; Lewis & Gilmore, 2007; López-Portillo et al., 2017).

## 4.2 | Climate change implications

Our map of mangrove observations points (Figure 1) is one of the first state-level spatial products to show the distribution of mangroves in Louisiana. In a warming world, we expect that the areas with high concentrations of mangrove observation points (e.g., the wetlands near Port Fourchon, Bay Junop, Caillou Bay, Isle Dernières, Timbalier Island, Grand Isle, Bay Melville, Bay Long and the Chandeleur Islands) will serve as hotspots for future mangrove expansion.

Since the last major freeze event occurred in 1989, *A. germinans* individuals in these areas have had thirty years to grow, expand, and become more resistant and resilient to future freeze events. Due to positive feedbacks between vegetation height and temperature, larger mangroves are typically more resistant to freezing temperatures than smaller mangroves (D'Odorico et al., 2010, 2013; Osland et al., 2015; Osland, Hartmann, et al., 2019; Weaver & Armitage, 2018). Larger mangroves also produce more propagules (Alleman & Hester, 2011), which can enhance the ability of mangrove populations to recover from freeze events via natural regeneration. During extreme freeze events, there can be dramatic vertical mangrove damage gradients due to temperature differences between air, water and soil; for example, air temperatures near the soil surface can be ~5°C warmer than at 25 cm above the soil surface (Osland, Hartmann, et al., 2019). As a result, mangrove propagules lying on the soil surface are often protected from freeze events by the buffering effects of warmer soil temperatures. So, following freeze events that kill more exposed mangrove seedlings and trees, mangrove natural regeneration can occur from the propagules lying on the soil surface. Increases in mangrove height, coverage and propagule production can foster positive vegetation–microclimate feedbacks (D'Odorico et al., 2013; Osland et al., 2015; Weaver & Armitage, 2018; Huang, Anderegg, Dawson, Mote & D'Odorico, 2020) that make the more abundant, taller and continuous mangroves present along the outer southeast Deltaic Plain coast even more resistant and resilient to future freeze events.

In response to warming winters in the coming century, we expect that mangroves will expand into Louisiana's interior Deltaic Plain and Chenier Plain; however, we do not expect that mangrove expansion will occur in a steady unidirectional manner. Rather, we expect that there will be pulses of rapid range expansion during freeze-free years followed by abrupt periods of range contraction after extreme freeze events. Due to the presence of vegetation–microclimate feedbacks, the rate of mangrove range expansion has the potential to accelerate during extended freeze-free periods (Osland et al., 2015). To complicate matters, mangrove range expansion will also be influenced by interactions with other aspects of climate change (McKee, Rogers, & Saintilan, 2012; Osland et al., 2018; Saintilan, Rogers, & McKee, 2019; Ward et al., 2016). For example, wetland loss and landward migration due to accelerated sea-level rise and saltwater intrusion will affect where mangroves can expand (Blum & Roberts, 2009; Conner, Doyle, & Krauss, 2007; Doyle, Krauss, Conner, & From, 2010; Enwright, Griffith, & Osland, 2016; Howard et al., 2020; Jankowski

et al., 2017). Hurricanes can facilitate the long-distance dispersal of mangrove propagules (Van der Stocken, Carroll, Menemenlis, Simard, & Koedam, 2019; Van der Stocken, Wee, et al., 2019), which will affect the spread of mangroves beyond their current distribution into the interior Deltaic Plain and Chenier Plain. Elevated atmospheric CO<sub>2</sub> concentrations can affect marsh–mangrove plant interactions (McKee & Rooth, 2008; Saintilan & Rogers, 2015). Extreme drought can lead to salt marsh dieback (i.e., brown marsh events; Michot, Wells, & Kemmerer, 2004; Michot, Kemmerer & Reiser, 2004; Alber, Swenson, Adamowicz, & Mendelssohn, 2008), which can reduce plant–plant competitive interactions and accelerate the rate of mangrove recruitment and growth within existing marshes (McKee, Mendelssohn, & Materne, 2004). Conversely, prolonged inundation of coastal wetlands due to extreme precipitation events and inland flooding can lead to marsh and mangrove dieback events. Collectively, these examples demonstrate the importance of considering interactions between climate change factors.

### 4.3 | Knowledge gaps, research needs and data limitations

In this study, we used the best available data to show that spatial variation in freeze frequency governs mangrove abundance, height and coverage in Louisiana. Our analyses provide a foundation for advancing understanding of climatic controls on the distribution of mangroves in one of the largest wetland complexes in the world. However, our work also shows that there is a need for improved state-level, remotely sensed mangrove coverage and structural (e.g., height, biomass) data for Louisiana and other mangrove range limits. Our climate-based approach for spatially depicting mangrove freeze damage risk and range expansion hotspots could easily be used in other mangrove range limits without robust mangrove presence data (e.g., north Texas, north Florida). We expect that this approach would be especially valuable for the Apalachicola region of northwest Florida, which has recently been a hotspot for expanding *A. germinans* and *R. mangle* individuals (Caitlin Snyder [Apalachicola National Estuarine Research Reserve], personal communication, 10 June 2019).

One notable limitation of our study is the use of mangrove data from 2009 given that our analyses of the frequency of extreme freeze events focus on a 30-year period (1989–2018). We would have preferred to have had mangrove data from 2018 or, even better, annual mangrove data for each of the 30 years. However, such data are not available. Thus, we used the best available data, assuming that the state-level distribution and structure of mangroves in Louisiana in 2009 was coarsely representative of the state-level distribution and structure in 2018. This assumption is valid for the large spatial extent at which this study was conducted (i.e., the entire Louisiana coast). Literature observations and herbarium records indicate that mangroves have been observed in very similar areas throughout much of the past century

(e.g., Grand Island, Isle Dernières, Chandeleur Islands). Indeed, in 2019, all 56 of the CRMS stations that contained *A. germinans* were located along the south-eastern outer coast within areas that had mangroves in 2009 and in areas that we identified as moderate or high freeze damage risk zones (i.e., green and yellow areas in Figure 5b).

Systematic statewide mangrove coverage data would have greatly improved our efforts. To better characterize temporal trends in mangrove expansion and growth near this dynamic range limit, temporal data are also needed to better quantify the spatio-temporal patterns of mangrove expansion (e.g., annual changes in mangrove coverage, height, biomass). Long-term in situ air temperature data measured within wetlands could also be used to complement the gridded temperature data and develop climate models that better characterize the influence of microclimatic gradients across Louisiana. Louisiana maintains one of the largest coastal monitoring networks in the world—the CRMS network (Steyer et al., 2003), which includes approximately 390 sites—however, air temperatures are not currently measured at CRMS sites. Improved knowledge of mangrove propagule dispersal is another critical knowledge gap (Van der Stocken, Carroll, et al., 2019; Van der Stocken, Wee, et al., 2019). Although the current mangrove distributional hotspots along the south-eastern outer coast of the Deltaic Plain produce large numbers of propagules, the travel pathways and fate of these propagules have been understudied (Alleman & Hester, 2011; Yando, 2018). Models of future mangrove expansion will require a better understanding of mangrove propagule dispersal across the Louisiana coast.

Although extreme freeze events across land–ocean temperature gradients play a critical role in restricting the distribution of mangroves in Louisiana, there are other concomitantly varying biotic and abiotic factors along these gradients that will also affect the future distribution and structure of mangroves. Within the context of mangrove expansion, these factors warrant additional consideration. For example, there are inundation, salinity and surface elevation change gradients across this zone that affect plant–plant interactions (Howard et al., 2015, 2017, 2020; Jiang et al., 2016). There are also concomitant gradients in mangrove propagule density, dispersal limitation and perhaps herbivory pressure, which may hinder rapid mangrove migration into interior areas that become climate-suitable. In less saline and more highly inundated wetlands that contain tall marsh vegetation, mangroves may not immediately be able to become established and compete for light and other resources. Mangrove establishment within these highly productive marshes may require ecological disturbances (e.g., drought, fire, prolonged inundation, hypersalinity, hurricanes, extreme grazing pressure) that lead to marsh vegetation dieback, producing space for mangrove dispersal, establishment and growth (McKee et al., 2004; Silliman, Van de Koppel, Bertness, Stanton, & Mendelssohn, 2005; Smith, Foster, Tiling-Range, & Jones, 2013). Thus, in addition to extreme freeze events, there are other abiotic and biotic factors that will modulate the rate and extent of mangrove expansion into interior wetlands in a warming world.

## 5 | CONCLUSIONS

Our analyses advance understanding of how the frequency of extreme freeze events controls the distribution, height and coverage of *A. germinans* near its northern range limit in wetland-rich Louisiana. *Avicennia germinans* is most abundant, tall and continuous along the south-eastern outer coast of Louisiana, where there is a lower risk of mangrove freeze damage (i.e., lower frequency of extreme freeze events). In contrast, the risk of *A. germinans* freeze damage has historically been very high across Louisiana's Chenier Plain and within more inland wetlands in the Deltaic Plain. In addition to informing climate-smart coastal restoration efforts, our findings can be used to better anticipate and prepare for the tropicalization of temperate wetlands due to climate change.

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## DATA AVAILABILITY STATEMENT

The data used in this study are all publicly available. The mangrove observation points are available in Day et al. (2020). The temperature data are available via the PRISM Climate Group (<http://www.prism.oregonstate.edu>). The Louisiana coastal vegetation type data are available in Sasser et al. (2014).

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**Author contributions:** All authors contributed to the study's conception and development. R.D. and T.M. collected the mangrove field data. R.D. formatted and prepared the mangrove spatial data for data release and subsequent analysis. M.O. obtained the climate data, conducted all data analyses, prepared the figures, and wrote the first manuscript draft. R.D. and T.M. contributed to subsequent manuscript drafts and gave final approval for publication.

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