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SHORT COMMUNICATION

Temperature Thresholds for Leaf Damage from Two Extreme Freeze Events (2018 and 2021) Near the Northern Range Limit of Black Mangroves (*Avicennia germinans*) in Southeastern North America

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Abstract
Extreme winter temperatures govern the northern range limit of black mangroves (*Avicennia germinans*) in southeastern North America. There is a pressing need for studies that advance our understanding of how extreme cold temperature events affect mangroves near their range limits. However, such events are infrequent and challenging to study at regional scales. Here, we compared the damage to mangroves from extreme freeze events in 2018 and 2021, using local data from sites in USA (Florida, Louisiana, and Texas) and northeastern Mexico (Tamaulipas). In 2018, mangrove damage was concentrated in Louisiana and the upper Texas coast, where minimum temperatures ranged from -4 °C to -7 °C. In 2021, damage from a more severe freeze event was concentrated along the central to northern coasts of Texas, where minimum temperatures ranged from -4 °C to -10 °C. We used regional temperature and vegetation data from these events to quantify temperature thresholds for *A. germinans* leaf damage. Our results indicate that *A. germinans* leaf damage is likely to occur when temperatures are between -4 °C and -6 °C. These findings help refine temperature thresholds for *A. germinans* leaf damage and advance understanding of the effects of extreme freeze events on mangrove range expansion. This information is valuable for anticipating future range dynamics in a warming world.

Keywords Mangrove · Range limit · Temperature thresholds · Freeze · Extreme event · Tropicalization

Introduction

Warming winter temperatures, attributed to climate change, are facilitating the range expansion of tropical species into temperate regions (e.g., Vergés et al. 2014; Osland et al. 2021). Within the tropical-temperate transition zone in North America, the frequency and intensity of extreme winter temperatures govern range expansion, distribution, and abundance of cold-sensitive tropical species. A particularly striking example occurs along the southeastern coast of the United States, where extreme winter storms delivering freezing temperatures to the coast dictate mangrove range expansion and contraction cycles (Sherrod and McMillan 1985; Everitt et al. 1996; Montagna et al. 2011; Osland et al. 2017; Cavanaugh et al. 2019). These freeze events can result in mangrove damage and, in the most extreme cases, landscape-scale mass mortality (Sherrod and McMillan 1981, 1985) (Fig. 1). Warming winters are expected to facilitate mangrove range expansion, leading to a shift from coastal wetlands dominated by graminoid and succulent salt marsh plants to mangrove forests. To better project transitions from temperate marsh to tropical mangrove forest under a changing climate, we need to advance our understanding of how extreme freeze events affect mangrove populations. However, studying the consequences of extreme freeze events on

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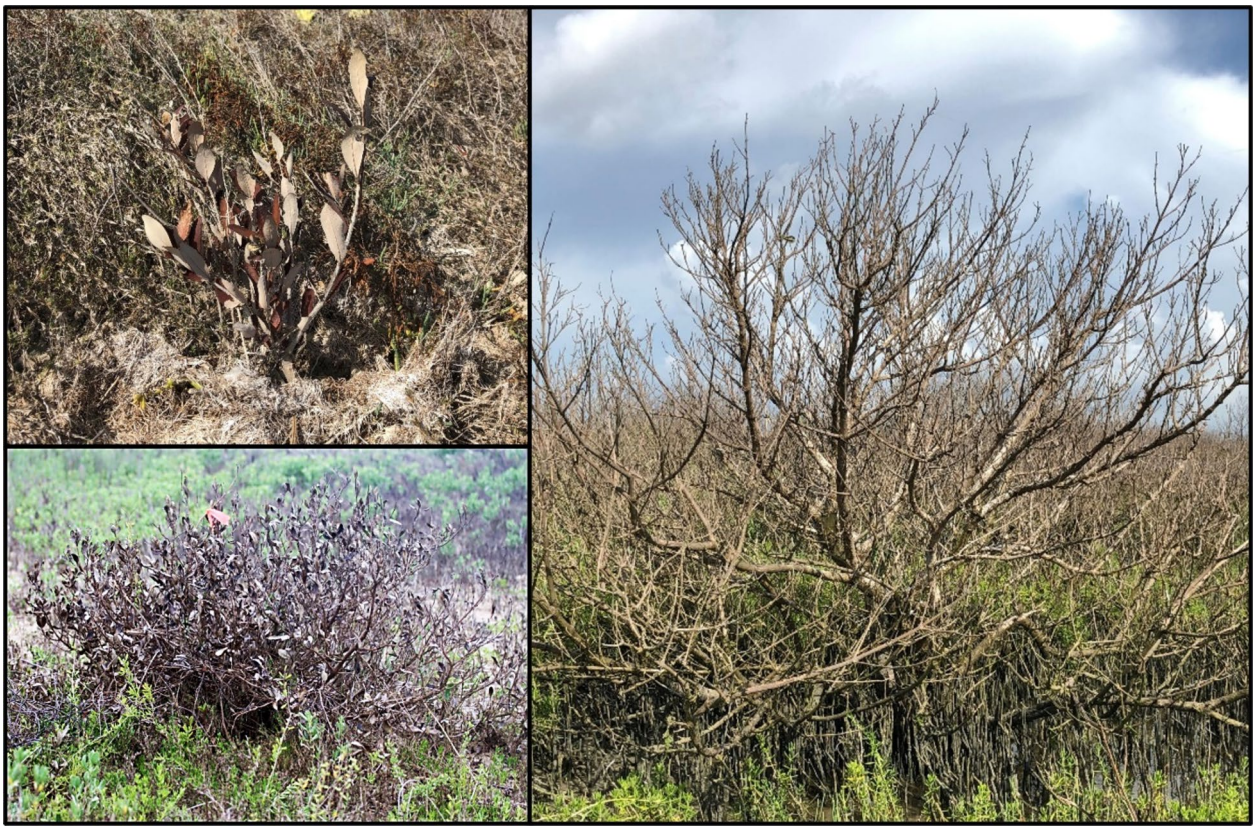

Fig. 1 Photos of freeze-damaged black mangrove (*Avicennia germinans*) individuals taken in Texas (USA) following the 2021 freeze event. The photos on the left were taken soon after the freeze event and show freeze-damaged, brown leaves that eventually fell from the tree. The photo on the right was taken six months after the freeze event and shows an individual with leafless and dead branches that have not resprouted. Following leaf loss during moderate freeze events, black mangrove individuals typically resprout vigorously from the stem, branches, and/or base of the plant. Photo credit: Simen Kaalstad

mangroves is challenging due to their infrequent and unpredictable occurrence. In this region, extreme freeze events occur on average only once every two to three decades (Osland et al. 2017; Cavanaugh et al. 2019; Snyder et al. 2021). Moreover, while some freeze events affect an entire region, others are localized to specific areas. To address this challenge and gain a better understanding of the spatial and temporal variability in freeze impacts to mangroves, we utilized local data collected by a coordinated collaborative network of individuals across the southeastern United States and northeastern Mexico.

In this study, we compared the effects of extreme freeze events in January 2018 and February 2021 on black mangroves (*Avicennia germinans*) in southeastern North America along the northern Gulf of Mexico and Atlantic Ocean coasts (Fig. 2). *Avicennia germinans* is the most cold-tolerant mangrove species in southeastern North America and extends the furthest north. Specifically, we investigated the following questions: (1) What were the temperatures experienced during the 2018 and 2021 events within coastal wetlands supporting *A. germinans*?; (2) Where were the coldest temperatures concentrated during the 2018 and 2021 events?; (3) What damage occurred to *A. germinans* during the 2018 and 2021 events?; and (4) Was the relationship between minimum temperature and mangrove freeze damage similar during the 2018 and 2021 events?

Methods

Study Area

We conducted this study along the northern Gulf of Mexico and Atlantic Ocean coasts (Fig. 2), near the northern range limit of mangroves in southeastern North America. This region is considered the coldest mangrove range limit in the world due to the extreme freeze events that affect mangroves (Lovelock et al. 2016; Osland et al. 2017; Cavanaugh et al. 2018). The most common and freeze-tolerant mangrove species in our study areas is the black mangrove (*Avicennia germinans*), which has been documented in this region since at least the 1700s and has fluctuated in abundance

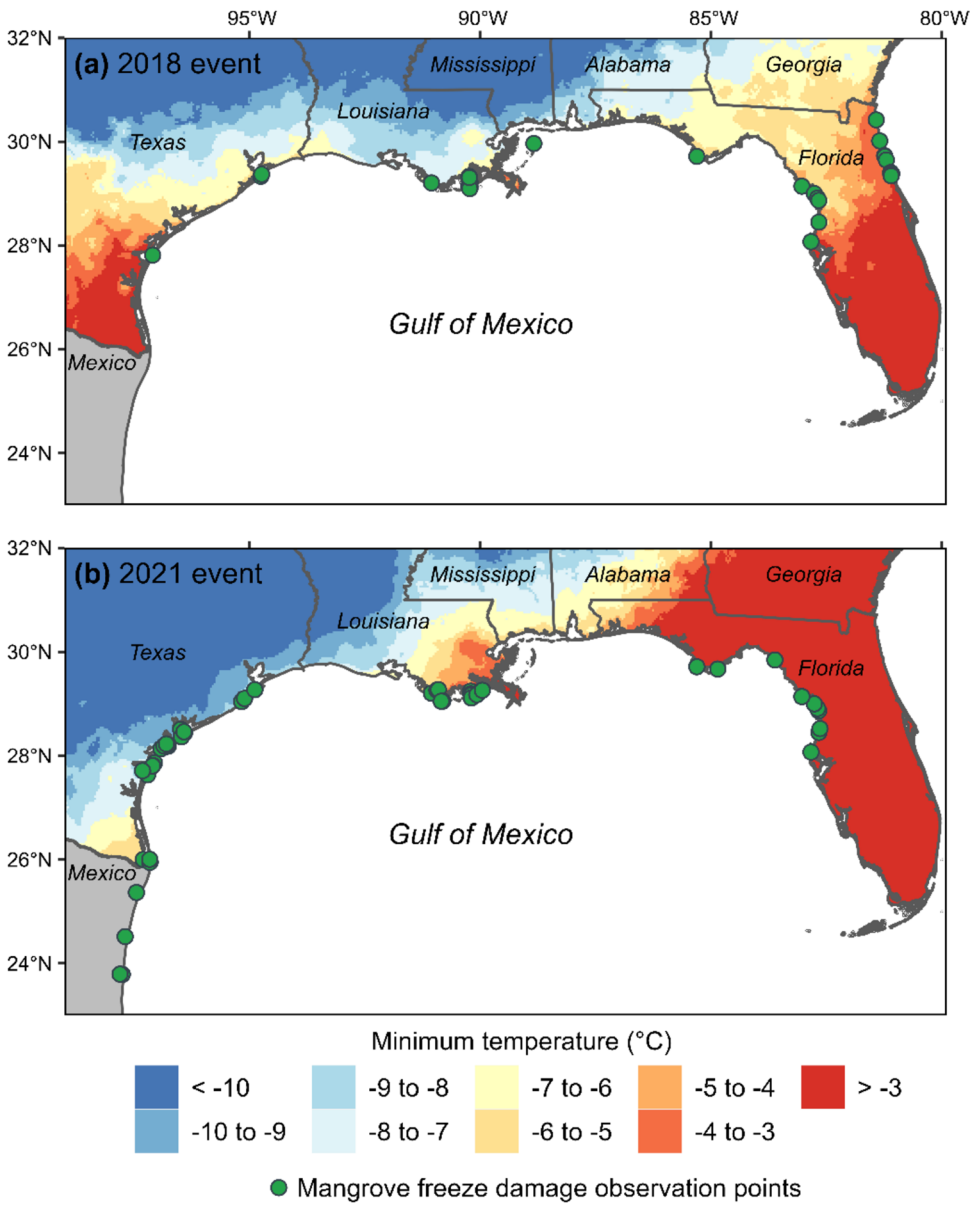

Fig. 2 Maps of the 23 and 75 mangrove freeze damage observation points and minimum air temperatures for the 2018 (**a**) and 2021 (**b**) freeze events, respectively. Note the differences in location and severity between the two events. During the 2018 event, mangrove damage was concentrated in Louisiana and northern Texas, where minimum temperatures ranged from -4 °C to -7 °C. In contrast, mangrove damage during the 2021 event was more severe and concentrated along the Texas coast, where minimum temperatures ranged from -4 °C to -10 °C. Minimum temperature data used in these maps were produced by the PRISM climate group (prism.oregonstate.edu)

and coverage in response to the frequency and intensity of extreme freeze events (Sherrod and McMillan 1981; McKee and Vervaeke 2018; Cavanaugh et al. 2019; Osland et al. 2020a). However, the red mangrove (*Rhizophora mangle*) is becoming increasingly common near mangrove range limits in Florida, USA (Snyder et al. 2021). Coastal wetland plant communities in the study area are typically dominated by freeze-tolerant salt marsh species, such as *Spartina alterniflora*, *Juncus roemerianus*, *Distichlis spicata*, *Batis maritima*, and *Salicornia spp.* (Stout 1984; Coldren and Proffitt 2017; Yando et al. 2016; Osland et al. 2019a, b). Nevertheless, mangrove abundance has increased, within salt marshes, near several range expansion hotspots in the southeastern United States, specifically in north Florida, Louisiana, and Texas, since the last major freeze event that caused mass mortality in 1989 (Osland et al. 2013; Armitage et al. 2015; Cavanaugh et al. 2019; McClenachan et al. 2021; Hesterberg et al. 2022; Bardou et al. 2023).

Study Sites

Following the 2018 event, we obtained leaf damage and temperature data from 23 sites across the region in Texas, Louisiana, and both coasts of Florida (Fig. 2a; Osland et al. 2020b). Following the 2021 event, we incorporated leaf damage data from 75 sites in Texas, Louisiana, Florida, and northeastern Mexico (Tamaulipas) (Fig. 2b; Kaalstad et al. 2023). Among the 75 sites from 2021, eight were located in northeastern Mexico (Fig. 2b), but we were only able to acquire temperature data for three sites closest to the

USA-Mexico border. As a result, we excluded five Mexico sites without temperature data from our analyses, reducing our study sample size for the 2021 event to 70 sites.

Temperature Data

We procured minimum temperature data, representing the absolute coldest recorded temperature during the events in 2018 and 2021 (Fig. 2). For the 2018 event, temperature data were sourced from Osland et al. (2020b), which included a combination of logger-based and gridded temperature data (at a 4 km resolution) generated by the PRISM climate group at Oregon State University (prism.oregonstate.edu). Gridded PRISM temperature data with a resolution of approximately 4 km were used for the 2021 event. A comparison and discussion of these different methods for temperature data collection can be found in Osland et al. (2020b). That study found moderate to strong linear relationships between logger-based and PRISM-based temperature data (R^2 ranging from 0.63 to 0.83, with slopes ranging from 0.84 to 1.30).

Leaf Damage Data

Mangrove leaf damage data for the 2018 and 2021 events were acquired from Osland et al. (2020b; 23 sites) and Kaalstad et al. (2023; 70 sites), respectively. Collaborators across the region collected leaf damage data following both events (Fig. 2b). At each site, collaborators visually estimated the percentage of leaves (ranging from 0 to 100%) exhibiting freeze damage on *A. germinans* individuals within 100-m^2 plots. The leaf damage measurements were collected within 2 months after the 2018 event and 2.5 months after the 2021 event. For some sites (i.e., 12 sites in 2018 and 10 sites in 2021), leaf damage for mangroves was estimated at the 100-m^2 plot level, indicating the percentage of leaves showing freeze damage for all mangrove individuals within the 100-m^2 plot. At other sites (i.e., 11 sites in 2018 and 60 sites in 2021), leaf damage for individual trees within a 100-m^2 plot was estimated, with 6 trees per plot in 2018 and 1–9 trees per plot in 2021. Individual tree measurements were then converted to plot-level means. Freeze-damaged leaves quickly turn brown and eventually detach from the tree (Osland et al. 2015, Fig. 1). Leaves that are partially damaged within the initial days following a freeze event eventually become fully damaged and fall from the tree. If a mangrove individual had all leaves showing partial damage, leaf damage was recorded as 100% for that individual. If the mangrove had already shed all its leaves at the time of sampling, leaf damage was recorded as 100%. For more detailed information about the ground-based leaf damage measurements, see Osland et al. 2020b and Kaalstad et al. 2023.

It is important to note that 100% leaf damage does not necessarily indicate mortality for *A. germinans* because this species can resprout vigorously from regenerative buds following moderate freeze events (Osland et al. 2015; Osland et al. 2020b; Feller et al. 2023). However, severe freeze events with temperatures below approximately -7 °C can lead to mortality (Osland et al. 2020b).

Data Analyses

Prior to conducting data analyses, we calculated the mean site-level mangrove leaf damage by averaging the data. These mean site-level data were used for subsequent analyses. Nonlinear logistic regression analyses were employed to determine the relationships between minimum temperature and mangrove leaf damage for three scenarios: (1) the 2018 event alone (23 sites); (2) the 2021 event alone (70 sites); and (3) the combined data from the 2018 and 2021 events. To identify leaf damage temperature thresholds (T) and threshold zones (AMRC – area of maximum rate of change), we utilized the first and second derivatives of the logistic equations. T was determined as the inflection point of the logistic equation, representing the location of the maximum rate of change and corresponding to the local maxima of the first derivative. AMRC was determined as the area between the local maxima and minima peaks of the second derivative of the logistic equation. This approach has been used successfully to quantify thresholds for plant damage, recovery, mortality, and distribution in previous studies (Osland and Feher 2020; Osland et al. 2020b, 2023). Data analyses were conducted in R version 4.0.5 (R Core Team 2021), and nonlinear logistic regression analyses were performed using nonlinear least squares (nls) and self-starting nls logistic models (SSlogis) within the R Stats Package.

Results

Minimum Temperatures

For coastal areas containing mangroves, the temperatures during the 2021 extreme freeze event were colder compared to the 2018 event (Fig. 2). Furthermore, the coldest temperatures during the two events were concentrated in different localized areas. During the 2018 event, the coldest temperatures impacting mangroves were observed in Louisiana and the north Texas coast (Fig. 2a), with minimum coastal temperatures ranging from -4 °C to -7 °C. In 2021, the coldest temperatures occurred along the northern and central Texas coasts (Fig. 2b), with minimum temperatures ranging from -4 °C to -10 °C.

Freeze-Induced Mangrove Leaf Damage

During the 2018 event, five of 23 sites experienced over 95% leaf damage, and these sites were all located along the Louisiana and north Texas coasts. In contrast, during the 2021 event, 35 of 75 sites exhibited over 95% leaf damage, and these sites were all located along the northern and central coasts of Texas.

Temperature Thresholds for Freeze-Induced Mangrove Leaf Damage

Significant non-linear negative relationships between minimum temperature and mangrove leaf damage were identified for both the 2018 and 2021 freeze events (Fig. 3a, b, respectively). During the 2018 event, the temperature threshold for leaf damage was determined to be -4.2 °C (Fig. 3a;

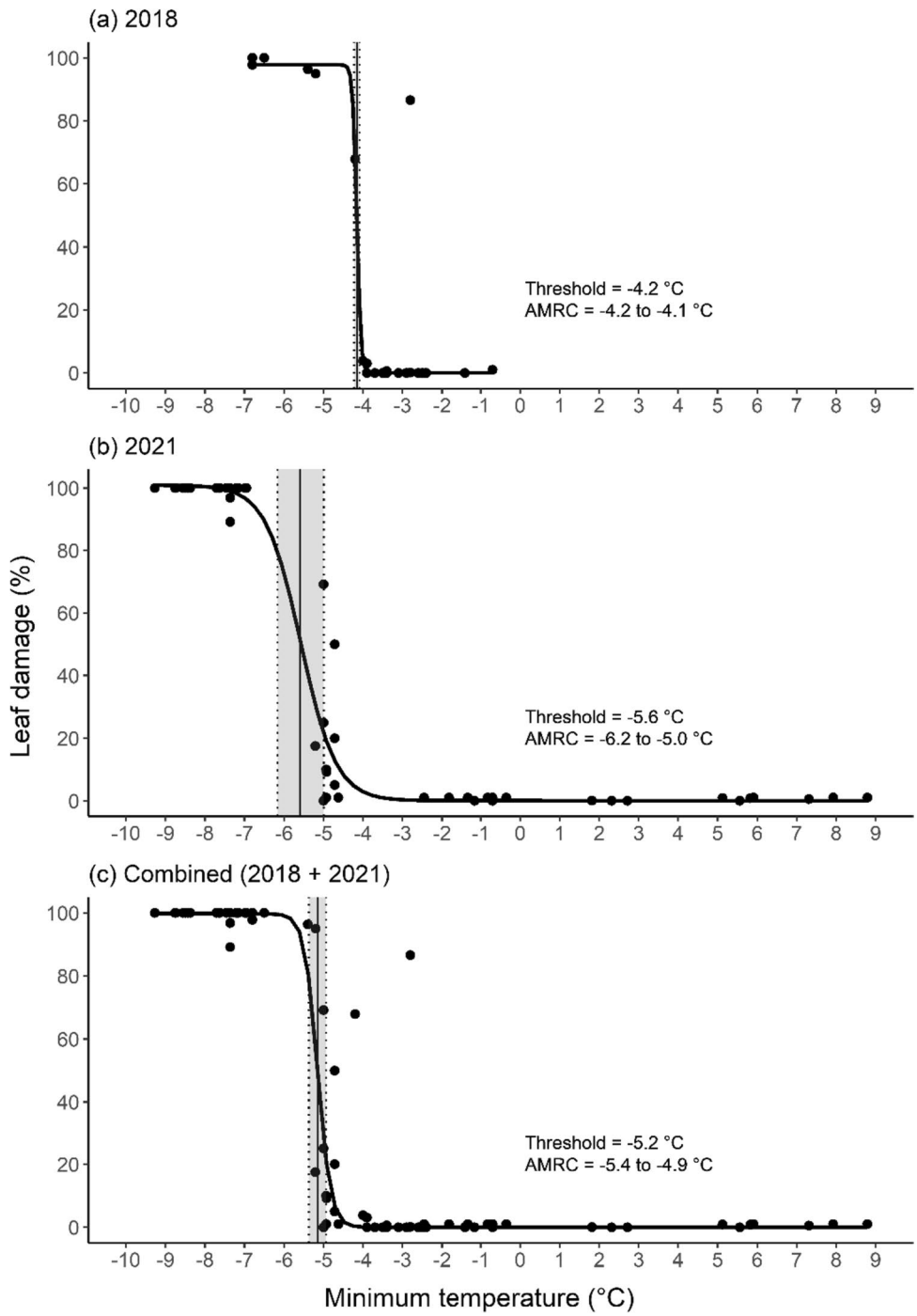

Fig. 3 The relationships between minimum air temperature (i.e., the coldest temperature during the event) and *Avicennia germinans* leaf damage for: **a** the 2018 freeze event alone; **b** the 2021 freeze event alone; and **c** both the 2018 and 2021 events together. The threshold values represent the minimum temperature thresholds for *A. germinans* leaf damage. The area of maximum rate of change (AMRC) represents the upper and lower boundaries of the threshold zone (vertical grey area bounded by dotted lines)

AMRC = -4.2 to -4.1 °C; RSE = 19.4; p = < 0.001). The temperature threshold for leaf damage during the 2021 event was -5.6 °C (Fig. 3b; AMRC = -6.2 to -5.0 °C; RSE = 8.8; p = < 0.001). When the data from the 2018 and 2021 events were combined, the temperature threshold for leaf damage was -5.2 °C (Fig. 3c; AMRC = -5.4 to -4.9 °C; RSE = 15.2; p = < 0.001).

Discussion

In this study, we compared temperature thresholds for mangrove leaf damage from two extreme freeze events (2018 and 2021) near the northern range limit of *A. germinans* in southeastern North America. Extreme freeze events are pulse disturbances that can cause wide-spread damage and mortality to mangroves, directly influencing mangrove range dynamics. While some extreme freeze events affect the entire southeastern USA region (e.g., the December 1989 freeze, which affected mangroves in Texas, Louisiana, and Florida), other freeze events are more localized (Rogers and Rohli 1991; Attaway 1997). For example, while the effects of the 2018 event were primarily isolated to the Louisiana and north Texas coasts (Osland et al. 2020a, b), the 2021 event affected the entire Texas coast (Martinez et al. 2023). Beyond spatial variation in impacts, our results show that temperatures during the 2021 event in Texas were colder than the 2018 event in Louisiana. The logistic regression model for the combined data includes the most heavily freeze-damaged mangroves from both event-specific areas, thus encompassing the intraspecific variability within the region and providing broader insight into mangrove damage during freeze events.

Combining the data from the 2018 and 2021 events indicates that *A. germinans* leaf damage is likely to occur when temperatures are between -4 °C and -6 °C. The temperature threshold for *A. germinans* leaf damage during the 2021 event was estimated to be 1.4 °C colder than during the 2018 event, which could be attributed to several factors. Differences in the temperature data are one potential cause. Although there is generally a strong correlation between gridded PRISM and logger-based temperature data, logger-based temperature data at certain sites can differ from PRISM-based data during extreme events (Osland et al. 2020b). Other factors that could play a role include differences in intraspecific cold tolerance (Pickens and Hester 2011; Madrid et al. 2014; Cook-Patton et al. 2015; Dangremond and Feller 2016; Hayes et al. 2020; Kennedy et al. 2020; Hoffman et al. 2022; Kennedy et al. 2022), freeze exposure, mangrove stand structure and coverage due to site environmental conditions (Yando et al. 2016; Simpson et al. 2017; Yando et al. 2018; Gabler et al. 2017; Weaver and Armitage 2018; Dangremond et al. 2020; Feller et al. 2023), life stage (Langston and Kaplan 2020; Macy et al. 2021), windspeed, and microclimate.

Microclimate greatly influences spatial and temporal variation in mangrove freeze damage and recovery in this region (Ross et al. 2009; Devaney et al. 2017; Osland et al. 2019a, b). The following six microclimatic factors significantly influence spatial patterns in mangrove freeze damage: (1) distance from the ocean, (2) distance from wind buffer, (3) mangrove canopy cover, (4) distance from soil surface, (5) local slope concavity, and (6) inundation (Osland et al. 2019a, b). Variation in microclimate can lead to local differences in mangrove freeze damage that could affect efforts to identify temperature thresholds using regional data.

The threshold values for *A. germinans* leaf damage identified in this study are close to temperature thresholds reported in the literature. In a laboratory freeze experiment, Cavanaugh et al. (2015) found that photoinactivation occurs near -3 °C. Following the 2018 event, Osland et al. (2020b) used field-based mangrove data to show that leaf damage occurs near -4 °C and mortality occurs near -7 °C. In an imagery-based study focused on mangroves in south, central, and north Florida, Cavanaugh et al. (2014) showed that reductions in mangrove area occur near -4 °C. In an imagery-based study focused on Louisiana mangroves, Osland et al. (2017) showed that reductions in mangrove area are linked to temperatures between -6 °C to -8 °C. In an analysis of temperature and coastal wetland distribution and land cover data, Osland et al. (2013) found that while mangrove presence is linked to minimum temperatures above -9 °C, mangrove dominance within coastal wetlands is most likely when minimum temperatures are above -7 °C.

Due to vigorous basal and epicormic resprouting, *A. germinans* individuals have a high capacity to recover from non-lethal freeze events (Osland et al. 2015; Osland et al. 2020b; Feller et al. 2023). Thus, physiological impacts to mangroves (e.g., leaf damage, photoinactivation) do not always result in mangrove mortality or lead to long-term reductions in mangrove coverage. When considering thresholds, it is important to distinguish between mangrove responses that lead to short-term impacts (e.g., short-term reductions in biomass) versus long-term impacts (e.g., mortality and reductions in mangrove coverage). Collectively, our results advance understanding of coastal wetland ecosystem responses to winter temperature extremes, which is critical information for anticipating future mangrove range dynamics in a warming world.

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Data Availability The 2021 data are available in Kaalstad et al. (2023). The 2018 data are available in the supporting file of Osland et al. (2020b).

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