


Temperature thresholds for black mangrove (*Avicennia germinans*) freeze damage, mortality and recovery in North America: Refining tipping points for range expansion in a warming climate

Michael J. Osland¹  | Richard H. Day¹  | Courtney T. Hall¹  | Laura C. Feher¹  |
Anna R. Armitage²  | Just Cebrian^{3,4}  | Kenneth H. Dunton⁵ | A. Randall Hughes⁶  |
David A. Kaplan⁷  | Amy K. Langston⁷  | Aaron Macy^{3,4,8}  | Carolyn A. Weaver²  |
Gordon H. Anderson⁹  | Karen Cummins¹⁰  | Ilka C. Feller¹¹  | Caitlin M. Snyder¹² 

¹U.S. Geological Survey, Lafayette, LA, USA; ²Texas A&M University at Galveston, Galveston, TX, USA; ³Dauphin Island Sea Lab, Dauphin Island, AL, USA; ⁴Department of Marine Science, University of South Alabama, Mobile, AL, USA; ⁵University of Texas Marine Science Institute, Port Aransas, TX, USA; ⁶Northeastern University, Boston, MA, USA; ⁷University of Florida, Gainesville, FL, USA; ⁸Mississippi State University, Biloxi, MS, USA; ⁹U.S. Geological Survey, Gainesville, FL, USA; ¹⁰Florida Forest Service, Tallahassee, FL, USA; ¹¹Smithsonian Environmental Research Center, Edgewater, MD, USA and ¹²Apalachicola National Estuarine Research Reserve, Eastpoint, FL, USA

Correspondence

Michael J. Osland

Email: mosland@usgs.gov

Present address

Just Cebrian, Northern Gulf
Institute, Mississippi State University,
Stennis Space Center, MS, USA

Amy K. Langston, Virginia Institute of
Marine Science, William & Mary, Gloucester
Point, VA, USA

Carolyn A. Weaver, Texas A&M University -
Corpus Christi, Corpus Christi, TX, USA

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Abstract

1. Near the tropical-temperate transition zone, warming winter temperatures are expected to facilitate the poleward range expansion of freeze-sensitive tropical organisms. In coastal wetlands of eastern and central North America, freeze-sensitive woody plants (mangroves) are expected to expand northward into regions currently dominated by freeze-tolerant herbaceous salt marsh plants. To advance understanding of mangrove range expansion, there is a need to refine temperature thresholds for mangrove freeze damage, mortality and recovery.
2. We integrated data from 38 sites spread across the mangrove range edge in the Gulf of Mexico and Atlantic coasts of North America, including data from a regional collaborative network – the Mangrove Migration Network. In 2018, an extreme freeze event affected 60% of these sites, with minimum temperatures ranging from 0 to -7°C .
3. We used temperature and vegetation data from before and after the freeze to quantify temperature thresholds for leaf damage, mortality and biomass recovery of the black mangrove (*Avicennia germinans*) – the most freeze-tolerant mangrove species in North America.
4. For *A. germinans* individuals near their northern range limit, our results indicate that temperature thresholds for leaf damage are close to -4°C , but temperature thresholds for mortality are closer to -7°C . Thresholds are expected to be warmer for more southern *A. germinans* individuals and for the other two common

mangrove species in the region (*Laguncularia racemosa* and *Rhizophora mangle*). Regenerative buds allowed *A. germinans* to resprout and recover quickly from above-ground freeze damage. Hence, biomass recovery levels during the first post-freeze growing season were 90%, 78%, 62% and 45% for temperatures of -4 , -5 , -6 and -7°C , respectively. Due to a combination of vigorous resprouting and new recruitment from propagules, we expect full recovery at most sites within 1–3 years, assuming no further freeze events.

5. *Synthesis.* To improve predictions of tropical range expansion in response to climate change, there is a need to better understand tropical species' responses to winter temperature extremes. Collectively, our results refine temperature thresholds for *A. germinans* freeze damage, mortality and recovery, which can improve predictions of mangrove range expansion and coastal wetland ecological transformations in a warming climate.

KEYWORDS

climate change, coastal wetland, freezing, mangrove forest, plant–climate interactions, range expansion, threshold, tropicalization

1 | INTRODUCTION

Climate change is altering the frequency and intensity of climate extremes (USGCRP, 2017), which is modifying the distribution of organisms and the structure and functioning of ecosystems (Jentsch, Kreyling, & Beierkuhnlein, 2007; Parmesan, Root, & Willig, 2000; Pecl et al., 2017; Smith, 2011; USGCRP, 2018). In addition to rising mean temperatures, climate warming is leading to an increase in the frequency and intensity of record maximum temperatures (e.g. extreme heat waves) as well as a decrease in the frequency and intensity of record minimum temperatures (e.g. extreme freezing and chilling temperatures). For some ecosystems, comparatively small changes in the frequency or intensity of climate extremes can produce abrupt and comparatively large ecological changes (i.e. ecological regime shifts; Folke et al., 2004; Scheffer & Carpenter, 2003). These rapid ecological transformations are often governed by climatic thresholds, and ecologists are increasingly challenged to identify where and when climatic-controlled tipping points may be crossed (Bahn, Reichstein, Dukes, Smith, & McDowell, 2014; Frank et al., 2015; Kayler et al., 2015; Ratajczak et al., 2018). Here we examined freezing temperature thresholds that control the range expansion of tropical woody plants (i.e. mangroves) in coastal wetland ecosystems of North America. Advancing understanding of plant sensitivity thresholds to freezing and chilling temperatures can help scientists and natural resource managers better anticipate and prepare for ecological transformations in a warming climate.

Most tropical organisms are sensitive to freezing and chilling temperatures (Boucek, Gaiser, Liu, & Rehage, 2016; Box, Crumpacker, & Hardin, 1993; Larcher, 2003; Sakai & Larcher, 1987; Woodward, 1987). Therefore, winter temperature regimes control the poleward distribution of most tropical biomes (Greller, 1980; Holdridge, 1967;

Whittaker, 1970). For example, in south Florida (USA), the northern range limits of tropical plant species are typically controlled by the frequency and intensity of freezing and/or chilling events, which are extreme climatic events that can kill plants and transform ecosystems. By the end of the century, warming winter temperature regimes due to anthropogenic climate change are expected to allow some freeze-sensitive tropical species to expand poleward into temperate biomes (Box, Crumpacker, & Hardin, 1999; Carter et al., 2018; Pecl et al., 2017; Vergés et al., 2014). In coastal wetlands, warming winter extremes are expected to allow freeze-sensitive mangrove forests to expand into freeze-tolerant salt marsh ecosystems (Cavanaugh et al., 2014; Osland, Feher, et al., 2017; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). Mangrove forest range expansion and the potential replacement of salt marsh ecosystems are landscape-level, ecological transformations that will have large ecological and societal ramifications (Guo et al., 2017; Kelleway et al., 2017). Hence, there is a need to advance understanding of the temperature thresholds that govern mangrove range expansion.

Winter temperatures greatly influence the ecological structure, function and distribution of mangrove forests in North America, Asia, Australia, New Zealand, South Africa and eastern South America; however, the ecological influence of winter temperature extremes (i.e. discrete freezing and/or chilling events) is strongest in eastern and central North America (Cavanaugh et al., 2018; Lovelock, Krauss, Osland, Reef, & Ball, 2016; Osland, Feher, et al., 2017; Stuart, Choat, Martin, Holbrook, & Ball, 2007). In North America, the black mangrove (*Avicennia germinans*; hereafter, black mangrove or *A. germinans*) is the most freeze-tolerant mangrove species. Of the three common mangrove species in the region, *A. germinans* is the species that extends furthest north where it expands and contracts in response to the absence or presence of winter air temperature extremes, respectively (Giri & Long, 2014; Osland

et al., 2018; Rodriguez, Feller, & Cavanaugh, 2016; Sherrod & McMillan, 1985). Within the past decade, several studies have demonstrated that winter temperature thresholds determine the northern range limit of *A. germinans* in eastern and central North America (Cavanaugh et al., 2014, 2015; Osland, Day, et al., 2017; Osland, Enwright, Day, & Doyle, 2013; Osland, Feher, et al., 2017). Despite the use of divergent data sources, methods and mangrove response variables, the temperature thresholds identified in those studies span a range between -3 and -9°C (Table 1). Most prior studies have relied on remotely sensed data of spatial or temporal changes in mangrove coverage; hence, there is a need for field-based freeze response studies that refine these temperature thresholds for mangrove biological responses to freezing.

In particular, there is a need to identify and contrast temperature thresholds for *A. germinans* freeze damage, mortality and biomass recovery. Regenerative buds allow *A. germinans* individuals to resprout and recover quickly from above-ground freeze damage (Tomlinson, 1986). Thus, distinguishing temperatures that result in short-term versus long-term damage would provide critical information for advancing understanding of freeze effects and for predicting future range dynamics. Leaf damage, for example, is potentially just a short-term freeze effect if leaf and biomass recovery occur rapidly within the first post-freeze growing season. In contrast, tree mortality is a longer-term freeze effect that can affect ecosystem stability if mangroves are removed from the system for multiple years or decades.

In this study, we integrated data from 38 sites spread across the mangrove range edge in the Gulf of Mexico and Atlantic coasts of the southeastern United States (Figure 1), including data from a regional collaborative network – the Mangrove Migration Network. A

recent freeze event provided a unique opportunity to refine temperature thresholds that ultimately regulate the speed of mangrove expansion into coastal salt marshes. The 2018 freeze event affected 60% of the 38 sites (see photos in Figure 2), with minimum temperatures ranging from 0 to -7°C . Here we used temperature and vegetation data from before and after the freeze to quantify specific temperature thresholds for *A. germinans* leaf damage, mortality and biomass recovery.

2 | MATERIALS AND METHODS

2.1 | Study area and overview

Our study was conducted near the northern range limit of mangrove species along the Gulf of Mexico and Atlantic Ocean coasts of North America (Figure 1). There are three common mangrove species in this region: *A. germinans* (black mangrove – the focal species for this study), *Rhizophora mangle* (red mangrove) and *Laguncularia racemosa* (white mangrove). Near these northern range limits, winter air temperature extremes greatly influence mangrove physiology (Cook-Patton, Lehmann, & Parker, 2015; Hayes et al., 2019; Madrid, Armitage, & López-Portillo, 2014; Stuart et al., 2007), reproduction (Dangremond & Feller, 2016) and architecture (Doughty et al., 2016; Feher et al., 2017; Simpson, Osborne, Duckett, & Feller, 2017; Yando et al., 2016). Freeze-tolerant salt marshes dominate areas that are too cold for mangrove forests, while mangroves dominate coastal reaches with mild winters. Hence, coastal wetlands in this region contain a dynamic mosaic of mangrove forest and salt marsh plants (Coldren, Langley,

TABLE 1 Studies that have quantified winter temperature thresholds that govern the northern range limit of *Avicennia germinans* (black mangrove) in eastern and central North America

Temperature	Response variable	Data type	Source
-3.2°C	Photoinactivation	Laboratory freeze experiment	Cavanaugh et al., 2015
-4.0°C	Area	Remotely sensed	Cavanaugh et al., 2014
-6.3 to -7.6°C	Area	Remotely sensed	Osland, Feher, et al., 2017
-7.0°C	Dominance	Remotely sensed	Osland et al., 2013
-8.9°C	Presence	Remotely sensed	Osland et al., 2013

Note: Despite divergent data sources, methods and mangrove response variables, the temperature thresholds identified in these studies span a range between -3 and -9°C .

FIGURE 1 Map of the 38 study sites and minimum air temperatures during the January 2018 freeze event. Minimum temperatures were obtained from data produced by the PRISM climate group (prism.oregonstate.edu)

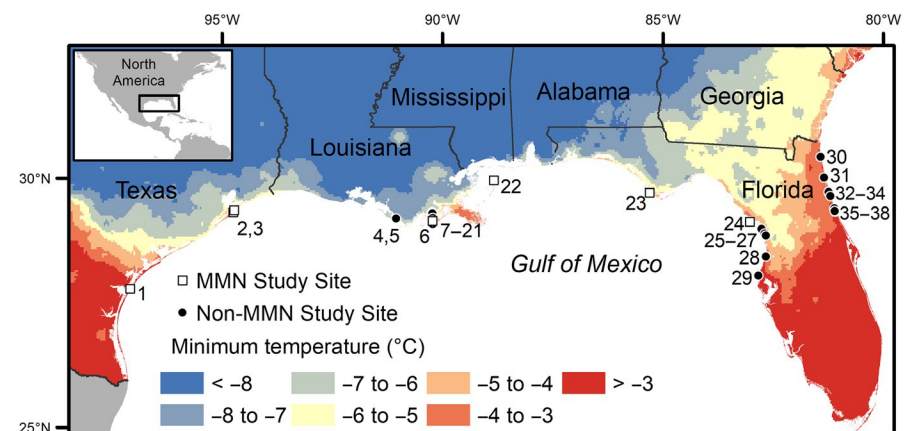




FIGURE 2 Photos of *Avicennia germinans* freeze damage (upper and middle photos), recovery (middle photos) and resistance (lower photos). The upper photos were taken the day that the freeze ended. Note the recently freeze-damaged, brown leaves in the upper photos. The middle photos were taken 9 months after the freeze event – near the end of the first post-freeze growing season – and show dead branches as well as recovery via resprouting branches from meristem reserve buds. The left, lower photo shows a mangrove stand in the area that was not freeze damaged, presumably due to a protective microclimate created by a wind buffer. The right, lower photo shows a mangrove propagule on the soil surface that was not damaged by the freeze event, presumably due to protective microclimate created by warmer temperatures near the soil surface

Feller, & Chapman, 2019; Langston, Kaplan, & Angelini, 2017; Macy et al., 2019; Perry & Mendelsohn, 2009; Weaver & Armitage, 2018).

This study was made possible by the collaborative contributions of scientists spread across the study area. Our analyses incorporate data from a total of 38 sites collected by nine organizations in three states and along two coasts (Figure 1). While some sites are part of a coordinated network that was in place before the freeze event (i.e. the Mangrove Migration Network), other sites were strategically added after the freeze event to capture additional freeze effects in targeted locations. Due to differences in the timing and form of data inputs, there is some variation in plot size, number of trees measured per plot, number of plots per site, and the amount and type of temperature and vegetation data recorded at each site; these differences are noted in

Tables S1–S3. For sites with tree- or plot-level data, the vegetation data were converted from tree-level data and/or plot-level data to site-level data using means of trees within plots and means of plots within sites. All subsequent analyses used site-level means.

2.2 | Study sites: mangrove migration network

Ecologically relevant freeze events do not occur every year in the study region (Osland, Feher, et al., 2017; Stuart et al., 2007). Therefore, knowledge of mangrove freeze damage and recovery dynamics has developed primarily from opportunistic observations conducted following freeze events (Lonard & Judd, 1991; Olmsted, Dunevitz, & Platt, 1993; Ross, Ruiz, Sah, & Hanan, 2009). To prepare for future freeze

events and better quantify the effects of winter temperature extremes upon mangroves near their northern range limit, a group of scientists working across the northern Gulf of Mexico launched the Mangrove Migration Network (MMN). This collaborative effort established a network of sites in 2014 along the northern range of mangrove distribution where plant community measurements could be collected consistently in concert with temperature measurements. Here we incorporate data from seven MMN sites – three in Texas (Port Aransas, Galveston and Bolivar), two in Louisiana (Port Fourchon and Chandeleur Island) and two in Florida (St. Joseph Bay and Cedar Key; Tables S1–S3). At each MMN site, we established 4–8 100-m² plots during the winter of 2014–2015. Within each MMN plot, we tagged a total of six trees for monitoring. We collected additional vegetation data at each site, but the MMN vegetation data presented here come exclusively from pre- and post-freeze measurements of the tagged trees.

2.3 | Study sites outside of the mangrove migration network

In addition to the seven MMN sites, our analyses incorporated data from 31 non-MMN sites (Tables S1–S3). Following the 2018 freeze event, the non-MMN sites were included to incorporate mangrove leaf damage, mortality and recovery data from additional locations along: (a) the Atlantic coast of Florida (nine sites between Cape Canaveral and St. Augustine); (b) the Gulf of Mexico coast of Florida (five sites between Cedar Key and Clearwater) and (c) Louisiana (two sites near Bay Junop and 15 sites between Golden Meadow and Port Fourchon). The 15 non-MMN sites in Louisiana between Golden Meadow and Port Fourchon span a land-ocean temperature gradient (Figure S1). Hereafter, we refer to these as the Louisiana gradient sites. During freeze events, mangrove damage and mortality are typically higher closer to Golden Meadow because temperatures are colder on the land side of this land-ocean temperature gradient (Osland, Day, et al., 2017; Osland, Hartmann, et al., 2019; Pickens, Sloey, & Hester, 2019). Conversely, mangrove damage and mortality are typically lower near and beyond Port Fourchon, where temperatures are warmer due to the proximity to the Gulf of Mexico.

2.4 | The January 2018 freeze event

January 2018 was a comparatively cold month in the southeastern United States, with several events producing freezing temperatures along the north-central Gulf of Mexico coast. The coldest event – the one with temperatures cold enough to lead to mangrove freeze damage and mortality – occurred between 17 and 19 January 2018. The Northern Texas, Louisiana, Mississippi, Alabama and northwest Florida coasts experienced the coldest temperatures during this event (Figure 1). On 19 January 2018 (i.e. the day after the focal freeze event for this study), RHD, MJO and LCF travelled to the Port Fourchon area to evaluate the impacts of the freeze. The patterns of leaf damage (i.e. recent damage; see upper left photo in Figure 2) enabled us to confidently attribute the damage and mortality to the event that occurred between 17 and 19 January 2018. The damage

at the Port Fourchon site prompted the request for data collection at the other 37 sites, and the site-specific timing of data collection are provided in Table S1.

2.5 | Freeze leaf damage data

Freeze-induced leaf damage was measured at 23 sites (Tables S1–S3). For each of these sites, we determined the mean *A. germinans* leaf damage (%). This value represents the per cent of leaves that were damaged by freezing temperatures. Freeze-damaged *A. germinans* leaves quickly turn brown and eventually fall from the tree (Osland et al., 2015). We used the contrast between green (live) and brown (freeze-damaged) leaves to visually estimate per cent leaf damage (i.e. brown leaf area divided by the sum of the brown leaf area and the green leaf area). The Port Fourchon MMN site was visited the day following the freeze event. The site-specific dates for leaf damage data collection are shown in Table S1.

2.6 | Freeze mortality data

We determined freeze mortality at 35 sites (Tables S1–S3). At 15 Louisiana gradient sites and three MMN sites (Galveston, Bolivar and Port Fourchon), we used mortality data collected near the end of the first post-freeze growing season (i.e. October–December 2018) to calculate per cent mortality (i.e. number of dead individuals divided by the total number of individuals). For the Anastasia site, per cent mortality was calculated using data collected in April 2019. We assigned a mortality value of 0% to the remaining 16 sites where leaf damage was less than 5% (i.e. where less than 5% of the leaves measured at the site were damaged); these sites did not have any freeze-induced mortality.

2.7 | Freeze biomass recovery data

Live but freeze-damaged *A. germinans* individuals will typically resprout vigorously from the base or stem of the plant. We quantified above-ground biomass recovery at 35 sites (Tables S1–S3). At freeze-damaged sites, we determined pre- and post-freeze above-ground biomass of individual trees using an allometric equation that incorporates measurements of height and two perpendicular crown diameters (Osland, Day, Larriviere, & From, 2014). We determined the pre-freeze biomass using measurements of pre-freeze height and crown diameters. Post-freeze biomass was determined using the same measurements conducted near the end of the first post-freeze growing season. For measurements of post-freeze biomass, we excluded any dead branches – only live portions of the plant were measured. We also measured the maximum height at which resprouting occurred (i.e. either from the base or the height of the tallest resprouting stem). At most freeze-damaged sites, per cent biomass recovery was calculated as the 2018 end-of-growing season above-ground biomass divided by the pre-freeze above-ground biomass. For the Anastasia site, this calculation was determined using post-freeze data collected in April 2019. Our use of the term biomass recovery thus represents the fraction of the post-freeze

biomass relative to the pre-freeze biomass and has a maximum value of 100% (Table S3). At 16 sites where leaf damage was less than 5%, we assigned a recovery value of 100% because the mangroves at these sites had retained and grown beyond their pre-freeze biomass. Including these sites in the analyses enabled us to characterize the position of the asymptote for the temperature–biomass recovery relationship. At the Louisiana gradient sites, we did not have measurements conducted before the freeze. However, repeated measurements at the Port Fourchon MMN site indicate that, in the absence of a major storm, the freeze-damaged, dead branches remain on the tree during much or all of the first year following a freeze (MJO and RHD, personal observations and measurements). Thus, at Louisiana gradient sites, dead branches were used to quantify pre-freeze biomass, and live branches were used to quantify post-freeze biomass.

2.8 | Temperature data

Logger-based in situ temperature data were not available for all sites (Tables S2 and S3). Hence, for temperature data, we relied on a combination of logger-based data and gridded daily minimum temperature data produced by the PRISM Climate Group at Oregon State University (prism.oregonstate.edu) using the PRISM (parameter–elevation relationship on independent slopes model) interpolation method (Daly et al., 2008). We chose the PRISM data because the PRISM model accounts for land–ocean temperature gradients (Daly et al., 2008; Daly, Helmer, & Quiñones, 2003; Daly, Widrlechner, Halbleib, Smith, & Gibson, 2012). The resolution of the PRISM data was 2.5 arcmin (~4 km). We used site coordinates to extract the corresponding daily minimum temperature for each site from the gridded PRISM data for 19 days (1–19 January 2018). For the freeze event (i.e. 17–19 January 2018), we used the site coordinates to extract the corresponding minimum temperature (i.e. the coldest temperature during the event) from the gridded PRISM data.

At six sites, we were able to obtain temperature data recorded using in situ temperature loggers (Tables S1 and S2). In 2014, we installed duplicate temperature loggers (HOBO U23-004; Onset Computer Corporation) at a height of 1-m above-ground within each MMN plot. Unfortunately, due to battery depletion and rodent damage, many of the temperature loggers installed at MMN sites were not operational during the 2018 freeze event. However, we were able to obtain logger-based temperature data from four MMN sites [Bolivar (two loggers), Port Fourchon (11 loggers), Chandeleur (four loggers) and St. Joseph Bay (three loggers)] and two non-MMN sites (one logger at each of the two Bay Junop sites). For these sites, we compiled daily logger-based and PRISM-based daily minimum temperature data for 19 days (1–19 January 2018; Table S4). For the freeze event that caused mangrove damage (i.e. 17–19 January 2018), we also determined the logger-based, event-specific minimum temperature (i.e. the coldest temperature recorded during the event). Then, we combined these event-specific logger-based data with the event-specific PRISM data to create a single dataset of the event-specific minimum temperature for all 38 sites. For the Galveston MMN site, which lacked logger data for this event, we

used logger data from the nearby Bolivar MMN site, which is less than 5 km away and in a direction that is parallel to the coast (i.e. not across a land–ocean temperature gradient).

2.9 | Data analyses: logger-based versus prism-based temperatures

We developed a dataset that could be used to evaluate the relationship between the logger-based and PRISM-based temperature data. First, we used means to convert the logger-based temperature data to plot-level, site-level and grid cell-level data. The two Bay Junop sites were located in the same grid cell. Hence, logger-based data from these two sites were averaged to produce a single grid cell-level mean. For each of five grid cells with logger data, we produced a dataset that contained logger-based and PRISM-based daily minimum temperature data for 1–19 January 2018 (Table S4). For each of these five grid cells, we used linear regression to evaluate the relationships between the logger-based and the PRISM-based temperature data. We also evaluated this relationship using combined data from all five grid cells.

2.10 | Data analyses: temperature–vegetation thresholds

We used sigmoidal regression analyses to evaluate the relationships between the event-specific minimum temperature (i.e. the combined PRISM and logger dataset) and the following site-level response variables: (a) per cent leaf damage, (b) per cent mortality and (c) per cent biomass recovery. Regression analyses were conducted in Sigma Plot (Systat Software). Spatial analyses were conducted in Esri ArcGIS (Environmental Systems Research Institute).

3 | RESULTS

3.1 | Freeze leaf damage

Of the 23 sites with data regarding leaf damage, the following seven sites had leaf damage due to freezing temperatures (data in parentheses represent per cent leaf damage): Junop1 (100%), Bolivar (100%), Galveston (98%), Port Fourchon (96%), Junop2 (95%), Anastasia (87%) and Chandeleur (68%). There was a negative sigmoidal relationship between minimum temperature and leaf damage (Figure 3a), and the temperature threshold for leaf damage was determined to be -4.2°C .

3.2 | Freeze mortality

Of the 35 sites with data regarding mortality, the following eight sites had some mortality following freezing temperatures (data in parentheses represent per cent mortality): Bolivar (75%), LA Gradient1 (60%), LA Gradient2 (33%), LA Gradient5 (33%), Galveston (28%), LA Gradient3 (20%), LA Gradient5a (11%) and Port Fourchon (4%). There was a negative sigmoidal relationship

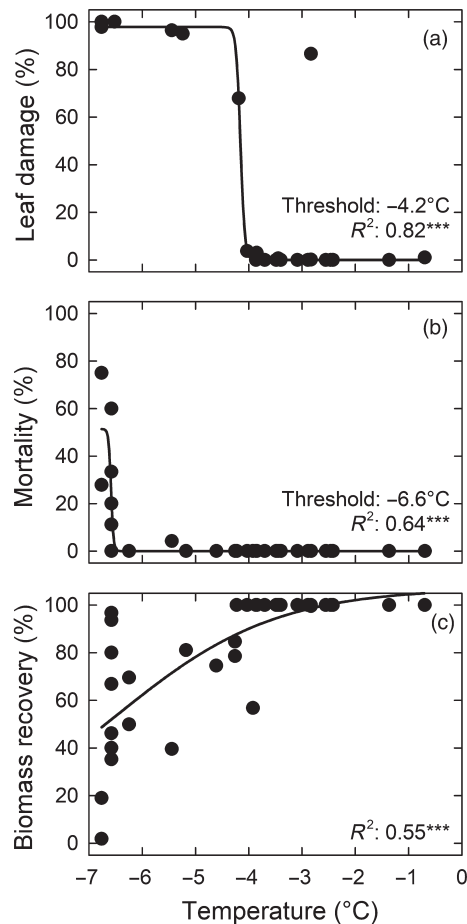


FIGURE 3 The relationships between minimum air temperature and *Avicennia germinans*: (a) leaf damage, (b) mortality and (c) biomass recovery near the end of the first post-freeze growing season. Threshold values in the upper (a) and middle (b) panels reflect the temperature thresholds for leaf damage or mortality, respectively. Temperatures represent a mixture of event-specific logger-based and PRISM-based data. Biomass recovery represents the fraction of the post-freeze biomass relative to the pre-freeze biomass. *** denotes p value significance less than .001

between minimum temperature and mortality (Figure 3b), and the temperature threshold for mortality was determined to be -6.6°C . Note that none of the sites had 100% mortality; even at the most affected sites (i.e. Bolivar and LA Gradient1), more than 25% of individuals were still alive.

3.3 | Freeze biomass recovery

Of the 35 sites with data regarding biomass recovery, there were seven sites that had biomass recovery percentages that were less than or equal to 50% by the end of the first post-freeze growing season (data in parentheses represent per cent biomass recovery): Bolivar (2%), Galveston (19%), LA Gradient2 (35%), Port Fourchon (40%), LA Gradient1 (40%), LA Gradient5 (46%) and LA Gradient6 (50%). There was a positive sigmoidal relationship between temperature and biomass recovery (Figure 3c). Based upon the equation

characterizing that relationship, biomass recovery levels by the end of the first post-freeze growing season were estimated to be 90%, 78%, 62% and 45% for temperatures of -4 , -5 , -6 , and -7°C , respectively.

3.4 | Maximum resprouting height

For individuals recovering from freeze-induced loss of above-ground biomass, the maximum height at which resprouting occurred ranged from 0 to 123 cm above the soil surface. Across all 15 sites where this metric was measured, the mean \pm SE maximum resprouting height was 31 ± 8 cm. At Louisiana gradient sites, the mean \pm SE maximum resprouting height was 37 ± 10 cm. The Bolivar and Galveston sites had the lowest resprouting heights – of the recovering individuals at these two sites, all but one of the individuals were resprouting from the plant base (i.e. the mean maximum resprouting height was 0 cm for both sites).

3.5 | Logger-based versus prism-based temperatures

For the five grid cells that had both logger-based and PRISM-based temperature data, there were moderate to strong linear relationships between both data sources (Figure S2: R^2 ranging from .63 to .83; slopes ranging from .84 to 1.30). In general, the PRISM data adequately represented the minimum temperatures at sites. However, there were several instances where the logger-based data differed from the PRISM data (Figure S2). For the freeze event of interest (i.e. the 17–19 January 2018 event), the site-specific differences between the logger-based and PRISM-based minimum temperatures were as follows, with positive or negative values indicating that the logger-based data were warmer or colder than the PRISM-based data, respectively: Junop1 (0°C), Port Fourchon (-0.8°C), Chandeaur ($+0.8^{\circ}\text{C}$), Junop2 ($+1.2^{\circ}\text{C}$), St. Joseph Bay ($+1.6^{\circ}\text{C}$) and Bolivar (-2.6°C ; Table S3).

4 | DISCUSSION

4.1 | Temperature thresholds

Advancing understanding of the ecological effects of climate extremes can be challenging because climate extremes are by definition infrequent (Jentsch et al., 2007; Smith, 2011), which means that ecologists seldom have the opportunity to directly observe and study the in situ ecological impacts. In the southeastern United States, for example, the last major, regionally significant freeze event occurred almost three decades ago – in December 1989, when temperatures fell to approximately -10°C near the northern range limit of mangroves (Lonard & Judd, 1991; Osland, Day, et al., 2017). Because such freeze events are infrequent, the ecological effects of winter temperature extremes in the region have historically been overlooked (Boucek et al., 2016; Osland et al., 2016), and scientists are often not fully prepared to rapidly redirect and mobilize

resources to study the influence of irregular, unpredictable freezing and chilling events.

Our coordinated effort across 38 sites in three states along two coasts showed that while temperature thresholds for *A. germinans* leaf damage are close to -4°C , tree mortality begins to increase at temperatures closer to -6.6°C . However, even at temperatures near -7°C , *A. germinans* mortality rates were still not 100%, indicating that temperatures below -7°C , perhaps somewhere in the range of -7 to -10°C , would be required for complete stand mortality (i.e. where all *A. germinans* individuals die and there is no biomass recovery from resprouting trees).

Regenerative buds allow *A. germinans* individuals to resprout and recover quickly from moderate levels of above-ground freeze damage (Lugo & Patterson-Zucca, 1977; Tomlinson, 1986). In our study, biomass recovery levels during the first post-freeze growing season were high. Our results indicate that freeze events with temperatures between -4 and -7°C can result in leaf loss, some mortality and some loss of above-ground biomass; however, these are short-term effects from which most mangrove stands and individuals can recover and regain lost biomass within 1–3 years, with no changes in mangrove area. Longer-term effects would likely occur at temperatures below -7°C , which is when we expect that ecosystem stability and mangrove aerial coverage would be affected by landscape-scale mortality. These findings are supported by historical analyses of aerial imagery from the mangrove-marsh ecotone near Port Fourchon, Louisiana, which indicate that temperatures near -10°C in the 1980s resulted in widespread mangrove mortality and landscape-level reductions in mangrove area; however, freeze events with temperature above -6°C in the 1990s and 2000s produced no decreases in mangrove area (Osland, Day, et al., 2017).

How do these thresholds compare to those for other mangrove species in eastern and central North America? The temperature thresholds identified in this study are for *A. germinans* individuals near their northern range limit along the Gulf of Mexico and Atlantic coasts of North America. Temperature thresholds are expected to be warmer for more southern *A. germinans* individuals (e.g. those in south Florida) because southern individuals are less frequently exposed to freezing and chilling temperatures (Cook-Patton et al., 2015; Hayes et al., 2019; Markley, McMillan, & Thompson Jr, 1982). Temperature thresholds would also be warmer for the other two common and less freeze-tolerant mangrove species in North America (i.e. *L. racemosa* and *R. mangle*; Coldren & Proffitt, 2017; Lugo & Patterson-Zucca, 1977; Olmsted et al., 1993). For example, chilling temperatures (i.e. 0 – 3°C) in South Florida were sufficient to cause damage to *L. racemosa* and *R. mangle* individuals (Ross et al., 2009; Zhang, Thapa, Ross, & Gann, 2016).

How do these thresholds compare to those for other mangrove species on other continents? The freezing temperatures affecting mangroves in the southeastern United States are the coldest temperatures reported globally; thus, the northern range limit of *A. germinans* in eastern and central North America is the coldest mangrove range limit in the world (Cavanaugh et al., 2018; Lovelock et al., 2016; Osland, Feher, et al., 2017; Stuart et al., 2007). Temperature

thresholds for other mangroves near poleward range limits on other continents are expected to be warmer than the thresholds identified here. In general, mangroves near range limits in the southern hemisphere (i.e. New Zealand, Australia, South Africa and eastern South America) are more strongly influenced by winter temperature means (i.e. consistently cold temperatures throughout most of the winter) rather than extremes. In contrast, mangroves near range limits in the northern hemisphere (i.e. China and North America) are more affected by winter temperature extremes (i.e. discrete freezing or chilling events that may last for just a few days or weeks despite warmer temperatures through the rest of the winter). Our understanding of species- and range-limit specific differences in mangrove physiology and sensitivity to freezing could be enhanced by the development of a global-scale mangrove migration network in combination with common garden freeze-exposure studies that incorporate species from different range limits across the world (Chen et al., 2017; Cook-Patton et al., 2015; Hayes et al., 2019; Madrid et al., 2014; Stuart et al., 2007).

There are several limitations to our study that can be improved with future efforts. While our analyses focus on freezing intensity (i.e. absolute minimum temperatures), the duration of freezing temperatures also influences plant physiological responses to winter temperature extremes (Attaway, 1997; Larcher, 2003). Microclimatic factors and life stage effects also add complexity to the identification of temperature thresholds for mangrove freeze damage and mortality (Devaney, Lehmann, Feller, & Parker, 2017; Osland, Hartmann, et al., 2019; Ross et al., 2009). Due in part to the influence of microclimatic gradients, freeze effects on *A. germinans* individuals are life stage dependent, where taller trees are more resistant to freezing temperature than shorter trees (Osland et al., 2015). However, low-lying mangrove seedlings and propagules near the soil surface can be protected from freezing temperatures due to the buffering effects of warmer soil temperatures and dense mangrove and salt marsh vegetation (Devaney et al., 2017; Lugo & Patterson-Zucca, 1977; McMillan & Sherrod, 1986; Pickens & Hester, 2011). Data from vertically positioned temperature loggers indicate that during freeze events, temperatures near the soil surface can be $\sim 5^{\circ}\text{C}$ warmer than temperatures at heights just 25 cm above the soil surface (Osland, Hartmann, et al., 2019). This means that, during most freeze events, plants near the soil surface may be exposed to much warmer temperatures than taller strata, which are exposed to colder, more hostile temperatures above. Vertical obstructions to wind can also create local shelter, where mangroves are protected from freezing temperatures (Liu, Liu, Liu, Li, & Wang, 2014; ARA, RHD, MJO personal observation), and tidal flooding can insulate and protect basal meristems from freeze damage (Chen et al., 2017; Wang, You, Wang, Huang, & Wang, 2011). Collectively, these microclimate gradients indicate that, as in many other woodland-grassland ecotones, there are positive vegetation-microclimate feedbacks that influence mangrove range expansion and sensitivity to winter temperature extremes (D'Odorico et al., 2013).

4.2 | Under the shadow of regional climate change

What are the implications of our findings for mangrove range dynamics due to climate change? In response to warming winter temperature extremes (USGCRP, 2017), mangroves and other tropical organisms are expected to move northward into more temperate biomes in eastern and central North America (Carter et al., 2018; Cavanaugh et al., 2014; Osland et al., 2013; Osland & Feher, 2019). In combination with temperature projections and models of mangrove propagule dispersal (Van der Stocken, Carroll, Menemenlis, Simard, & Koedam, 2019; Van der Stocken, Wee, et al., 2019), establishment (Krauss et al., 2008), and growth (Berger et al., 2008), the temperature thresholds identified for *A. germinans* leaf damage, mortality and biomass recovery can be used to help scientists and natural resource managers better anticipate mangrove range dynamics in a warming world.

Within the past several decades, ecologists have increasingly demonstrated the importance of experimental climate change studies that investigate the influence of climate extremes (Jentsch et al., 2007; Knapp et al., 2015; Smith, 2011). Our efforts highlight the large benefits that can come from mobilizing and coordinating existing regional partnerships to advance understanding of extreme events near species' range limits. With coordinated and comparatively modest inputs from multiple scientists spread across a regional range limit, we were able to build a dataset that significantly advances understanding of the impacts of winter climate extremes on *A. germinans* range dynamics. In a rapidly changing world where climate change is redistributing species and leading to range limit expansions and contractions, our work demonstrates the value of coordinated, regional collaborations for quantifying the effects of climate extremes on species range limits.

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AUTHORS' CONTRIBUTIONS

M.J.O. and R.H.D. conceived the initial idea for the network. All authors contributed to study conception, design and/or data collection. C.T.H. helped collaborators establish Mangrove Migration Network plots. L.C.F., C.T.H. and M.J.O. managed and organized the data. M.J.O. analysed the data and wrote the first manuscript draft. All authors contributed to subsequent manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data is available from Osland et al. (2019) <https://doi.org/10.5066/P9WUX46Y>.

ORCID

Michael J. Osland  <https://orcid.org/0000-0001-9902-8692>
 Richard H. Day  <https://orcid.org/0000-0002-5959-7054>
 Courtney T. Hall  <https://orcid.org/0000-0003-0990-5212>
 Laura C. Feher  <https://orcid.org/0000-0002-5983-6190>
 Anna R. Armitage  <https://orcid.org/0000-0003-1563-8026>
 Just Cebrian  <https://orcid.org/0000-0002-9916-8430>
 A. Randall Hughes  <https://orcid.org/0000-0001-5072-7310>
 David A. Kaplan  <https://orcid.org/0000-0002-0103-0928>
 Amy K. Langston  <https://orcid.org/0000-0002-2402-8898>
 Aaron Macy  <https://orcid.org/0000-0003-2170-6240>
 Carolyn A. Weaver  <https://orcid.org/0000-0002-1447-6371>
 Gordon H. Anderson  <https://orcid.org/0000-0003-1675-8329>
 Karen Cummins  <https://orcid.org/0000-0001-7618-9303>
 Ilka C. Feller  <https://orcid.org/0000-0002-6391-1608>
 Caitlin M. Snyder  <https://orcid.org/0000-0002-9202-2148>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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