



Ongoing Range Shift of Mangrove Foundation Species: *Avicennia germinans* and *Rhizophora mangle* in Georgia, United States

William C. Vervaeke¹ · Ilka C. Feller² · Scott F. Jones³

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Abstract

Climate change is leading to shifting vegetation patterns in coastal areas worldwide. One such shift in vegetation is the ability of tropical species to establish and survive poleward of recent historical distributions. A well-studied example of this tropicalization is the expansion of mangroves into saltmarshes, creating a marsh-mangrove ecotone thought to be controlled by a decrease in extreme freeze events in the southeastern USA. However, accurate mangrove distribution data at their northern limit in this region are currently lacking. Here, we report information collected from targeted surveys along the Atlantic coasts of Florida and Georgia at the northern limit of mangroves in the USA. We document both *Avicennia germinans* and *Rhizophora mangle* individuals naturally occurring in Georgia, poleward of previous reports by more than 23 km (*A. germinans*) and by almost 80 km (*R. mangle*), respectively. Our results highlight the lack of distributional information in this under-sampled region and the need for additional study of species-specific physiology and tolerance, especially for *R. mangle*, which exhibited surprising resilience and responses to freeze events. These data will be crucial to validate models showing a northern shift of mangroves. Knowing where mangroves have been established and the associated conditions that allowed establishment will help inform models of tropicalization and ecotonal shifts in areas where foundation species are expanding, giving managers and researchers the needed insight as current landscapes change.

Keywords Saltmarsh · Mangrove · Ecotone · Tropicalization · Range shift · Climate change

Introduction

Climate change is altering environmental conditions and causing range shifts of foundation species through the tropicalization of temperate areas (Bates et al., 2014; McLean et al., 2021; Osland et al., 2021). Tropicalization, caused by decreases in the frequency of extreme cold events, may be a major factor driving latitudinal shifts of foundation species within some temperate-tropical ecotones (Osland et al., 2021; Parmesan et al., 2000). The marsh-mangrove ecotone

in particular may be an ideal study system for investigating tropicalization, as it occurs along the border of potentially expanding tropical climates and has a visible foundation for species change when conditions shift (Osland et al., 2023). In the southeastern USA, where increased minimum temperatures may be a contributing factor driving mangrove expansion, climate projection models suggest a 5 °C increase in annual temperature minima by 2100, and given sufficient dispersal and available habitat, such increases in minimum temperature and associated lack of lethal freeze events could potentially allow mangrove distribution to expand as far north as South Carolina, United States (Cavanaugh et al., 2019). Projecting future climate is complex, and additional destabilization of the polar vortex and jet stream may lead to potential lethal freeze events, though the evidence is mixed (Domeisen, 2019; Zhang et al., 2020). In contrast to the southeastern United States, other regions including those in the Southern Hemisphere are experiencing mangrove expansion from non-temperature drivers, including estuarine geomorphology (Raw et al., 2019; Whitt et al., 2020) and relative sea-level rise (Saintilan et al., 2019).

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✉ William C. Vervaeke
william_vervaeke@nps.gov

¹ Southeast Coast Inventory and Monitoring Network, National Park Service, 135 Phoenix Road, Athens, GA 30605, USA

² Smithsonian Environmental Research Center, 647 Contees Wharf Rd, Edgewater, MD 21037, USA

³ Department of Biology, University of North Florida, 1 UNF Drive, Jacksonville, FL 32224, USA

The southeastern United States has a strong research base exploring the functional implications and drivers of ecotonal shifts with climate change (Osland et al., 2019; Rodriguez et al., 2016; Simpson et al., 2017). Due to rapidly changing environmental conditions and potential shifts in ecosystem function across an area with large expanses of saltmarsh habitat (Worthington et al., 2024), a regional approach to tracking species range shifts may be most useful, as demonstrated for expanding mangroves along the Gulf of Mexico coast of Florida (Snyder et al., 2022). Currently, this approach is lacking for the range limit of mangroves on the Atlantic Coast, despite evidence that mangroves in northeast Florida may respond most strongly to a warming climate at their poleward range edge (Chapman et al., 2021).

Reports of mangrove presence and abundance at this range limit are scarce, and the region is known to be under-sampled and under-reported (Bardou et al., 2023). Currently, the northernmost published mangrove patch location (*Avicennia germinans*, black mangrove) is at Fort George Inlet in the Timucuan Ecological and Historic Preserve in Jacksonville, Florida (Cavanaugh et al., 2019) with the northernmost individual on the southern tip of Amelia Island (Kennedy et al., 2020). These publications are a culmination of ongoing road surveys conducted from Georgia to northeast Florida since 2004 (I.C. Feller, pers. obs.). The northernmost reported *Rhizophora mangle* (red mangrove) is in the Guana Tolomato Matanzas National Estuarine Research Reserve (Frazel, 2009). Unpublished datasets have contained *A. germinans* and *R. mangle* as far north as the Nassau River in Duval County, Florida (W.C. Vervaeke, unpub. data), as part of newly established ongoing monitoring of mangrove populations led by the National Park Service. Despite these records, there remains a distinct data gap on the current distribution of the northernmost mangroves on Florida's Atlantic Coast (Bardou et al., 2023), which are the northernmost mangroves in the United States.

This gap is hindering the prediction of future mangrove expansion and the ecological effects of foundation species turnover. Here, we detail the results of field surveys of coastal areas poleward of the northernmost reported mangrove, aimed at filling mangrove distribution gaps at their range limit in Northeast Florida, conducted in 2024. We report both *A. germinans* and *R. mangle* as naturally occurring in Georgia, United States, at latitudes between 30.73 and 30.74° N.

Materials and Methods

Site Setting

The northern range limit of mangroves in the southeastern United States currently occurs near the Florida-Georgia

border. This border follows the St. Marys River, which ends between two barrier islands: Cumberland Island (north) and Amelia Island (south) (Fig. 1). This region marks a transition from bar-built lagoonal systems (St. Augustine, Florida southward) to riverine estuaries with back-barrier complexes (Jacksonville, Florida northward) (Dame et al., 2000). Marshes in the region are typically dominated by *Spartina alterniflora* in the low marsh, with *Juncus roemerianus* in the high marsh and in areas with brackish salinities (Dame et al., 2000; Odum, 1988). The area of Cumberland Bay is bordered on the west by Kings Bay Naval Base and the east by Cumberland Island, a National Park Service (NPS) designated National Seashore. In Florida, there are extensive marshes south of the St. Marys River along the Intracoastal Waterway (ICW). The mean tidal range in this area is 1.83 m, which are some of the largest tides in the southeast United States. The climate in this region is humid subtropical (Köppen Cfa; Beck et al., 2018), with average monthly low temperatures ranging from 3.9 to 21.7 °C (<https://www.usclimatedata.com/climate/jacksonville/florida/united-states/usfl0663>). The region sees frequent tropical storm systems, and although initial direct hits are rare, there have been eight storms that have tracked within 100 km of this region over the last 10 years (https://www.nhc.noaa.gov/data/#tracks_all).

Field Surveys and Data Collection

Surveys were conducted by small watercraft at high tide during winter when *Spartina* is senescent and evergreen mangrove shrubs are easier to locate. Once located, individuals were accessed by foot. Survey areas were bounded to the south by the northernmost known mangrove individuals (C. Vervaeke, unpub. data) and were constrained to navigable channels along the Amelia River, St. Marys River mainstem upstream to the Cumberland Island Ferry dock, and Cumberland Sound/East River north to Stafford. Surveys continued 10 km north of the northernmost located individuals to ensure reasonably complete coverage. Surveys in January and February 2024 were conducted between the Nassau River, Florida, and St. Marys River along the ICW (Fig. 1). Both surveys expanded to the north side of the St. Marys River in Georgia, with the February survey following Cumberland Island north to East River and west to Kings Bay Naval Base. A final survey was conducted in August 2024 to confirm the locations of the Georgia individuals and to collect additional data on the northernmost mangroves in Florida (Fig. 1).

Geodetic locations of individual mangroves were collected with Trimble Mobile Manager software using a Trimble R12i GNSS receiver. Positions are relative to the North American Datum of 1983 (NAD 1983 (2010.0)), and elevations are relative to the North American Vertical Datum

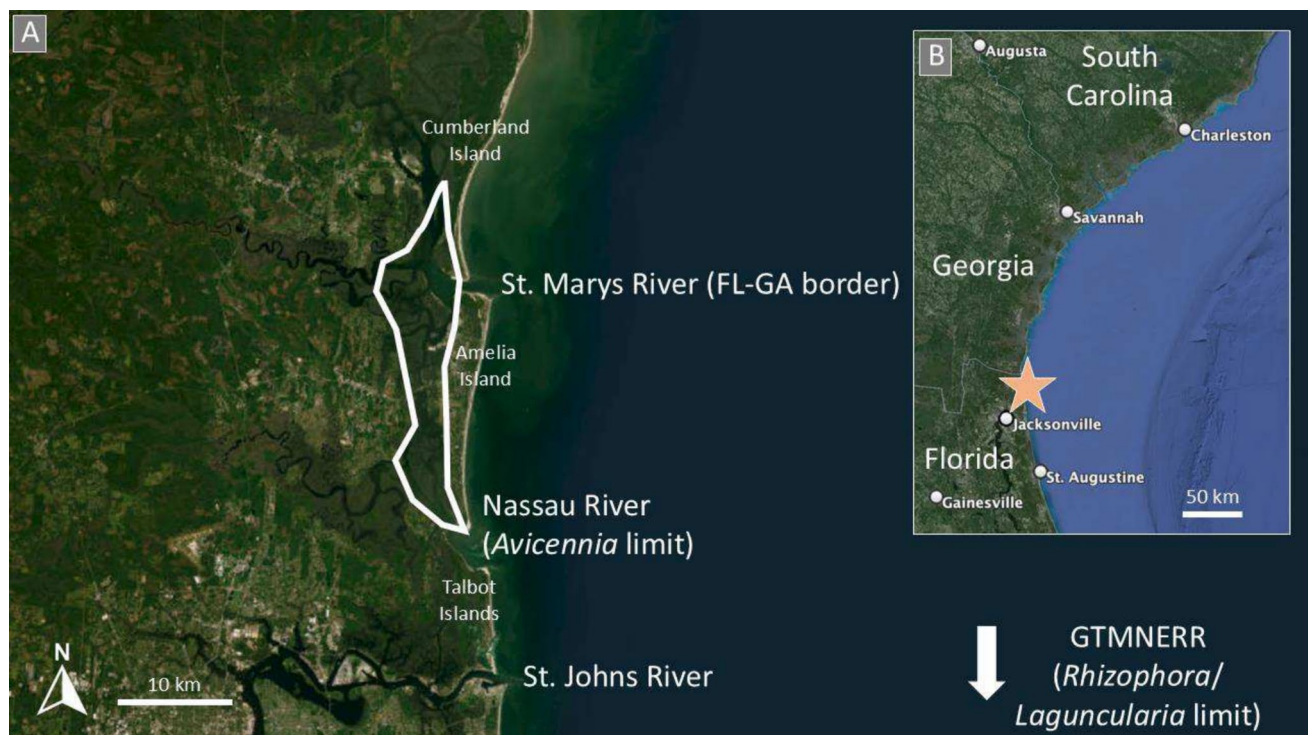


Fig. 1 (A) Map of study area with specific survey areas (white polygon) in Florida and Georgia, United States, and current northern distributional limits of mangrove species reported in the literature

(listed). (B) Regional setting in the southeastern United States (study area denoted by star)

of 1988 (NAVD88) using Geoid18. Corrections were completed in real-time kinematic (RTK) with minimum vertical precision of 0.02 m and minimum horizontal precision of 0.01 m.

Each mangrove reported was measured for total height (m), and two canopy diameter measurements (m) were collected at perpendicular angles as a metric of size and shape (Feller et al., 2023). Mangrove species identity and reproductive status were also noted by the presence of flowers, fruit, and/or propagules. To record the approximate age of each mangrove, we located annual increments of growth (leaf nodes) from branch tips to as close to the base of the plant as possible (Duarte et al., 1999; Feller et al., 2023).

Results

The northernmost *A. germinans* and *R. mangle* individuals were found in Georgia, with an *R. mangle* individual in the northernmost mangrove at 30.7353° N (Fig. 2, Table 1). The northernmost *A. germinans* individual is nearby, at 30.7314° N (Fig. 2, Table 1). Surveys in 2024 recorded a

total of eight *A. germinans* and 40 *R. mangle* individuals, all north of published mangroves and north of the previously known range limit of 30.5646° N along the Nassau River,

Florida (Vervaeke, unpub. data). Northernmost mangrove individuals were generally small and young (Figs. 3 and 4, Table 1). All *R. mangle* individuals reported here were shorter than 1.01 m and estimated to be younger than 5 years old. Most *A. germinans* individuals were similarly small and young, save for one large individual 1.33 m tall that was estimated to be greater than 5 years old.

Discussion

Naturally, recruited *A. germinans* and *R. mangle* individuals in Georgia provide evidence that mangroves may be establishing poleward of their historical range limits in the southeastern United States. This expansion is often attributed to anthropogenic climate change and associated global warming in this region, allowing these tropical plants to survive at more northern latitudes (Osland et al., 2021). Periodic freeze events are natural in this region and are expected to continue even as the overall climate warms (Cavanaugh et al., 2019). Other periodic disturbances, such as hurricanes, also influence the rate at which mangrove propagules disperse and affect their poleward expansion (Kennedy et al., 2020). Similar to the mangroves we report here, John Muir observed mangroves in 1867 growing in clumps in the coastal marshes

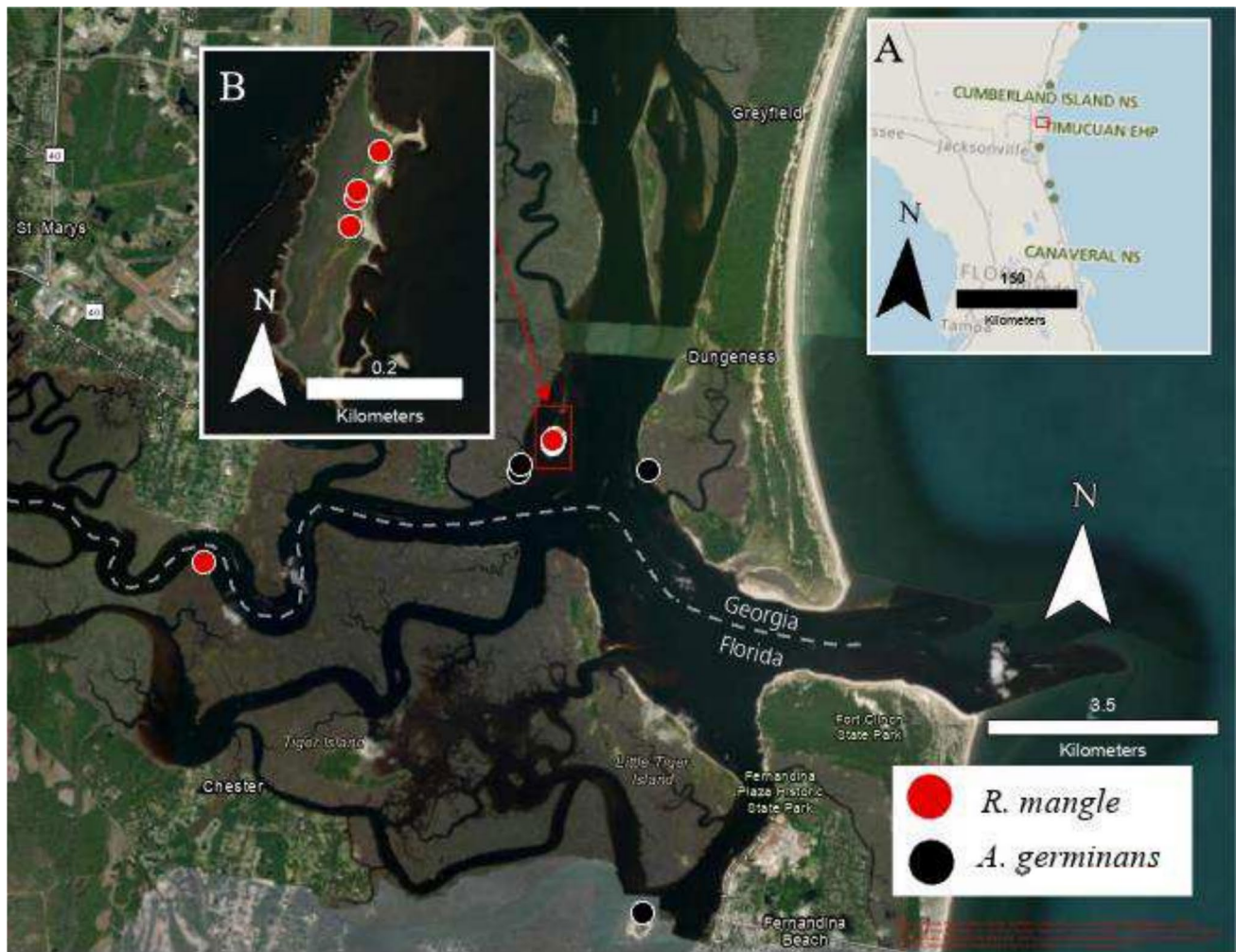


Fig. 2 Map of study area (inset (A)) and mangrove point data locations for *Rhizophora mangle* (red mangrove) and *Avicennia germinans* (black mangrove) at their current northern limit in Georgia,

United States. Inset map (B) more detailed location and distribution of Georgia *R. mangle* in Cumberland Bay

Table 1 Location, elevation, and plant structural data for all currently known mangroves of both *Avicennia germinans* (black mangrove) and *Rhizophora mangle* (red mangrove) in Georgia and the northernmost mangroves in Florida, United States

Location	Species ID	Location (lat, long)	Elevation (m NAVD88)	Height (m)	Canopy diameter (m)	Age (years)	Reproductive status
Georgia	<i>R. mangle</i>	30.73529, −81.49527	0.798	0.74	0.40, 0.33	4	Y (flowers and fruit)
	<i>R. mangle</i>	30.73479, −81.49554	0.889	0.57	0.29, 0.28	3	Y (flowers)
	<i>R. mangle</i>	30.73471, −81.49557	0.876	0.45	0.23, 0.19	3	N
	<i>R. mangle</i>	30.73438, −81.49561	0.754	0.69	0.58, 0.44	4	N
	<i>A. germinans</i>	30.73139, −81.50038	0.693	0.80	0.46, 0.34	4	N
	<i>A. germinans</i>	30.73152, −81.48027	0.717	0.76	0.30, 0.22	3	N
	<i>A. germinans</i>	30.73030, −81.50053	0.809	1.33	1.66, 1.49	5 to 7	Y (propagules)
Florida	<i>R. mangle</i>	30.71560, −81.54883	0.784	1.01	0.37, 0.28	4	Y (flowers))
	<i>A. germinans</i>	30.67149, −81.47694	0.799	0.70	1.55, 1.48	> 5	Y (flowers)

Fig. 3 Photographs of *Rhizophora mangle* (red mangrove) individuals in early 2024 from Georgia, United States. Photo credits: **A, B** S.F. Jones, University of North Florida

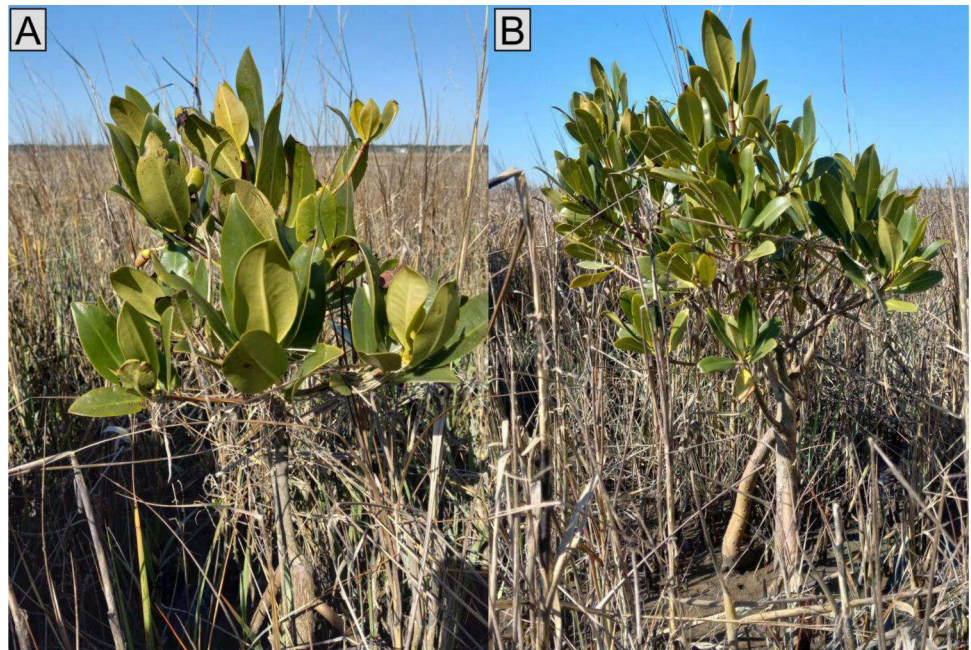
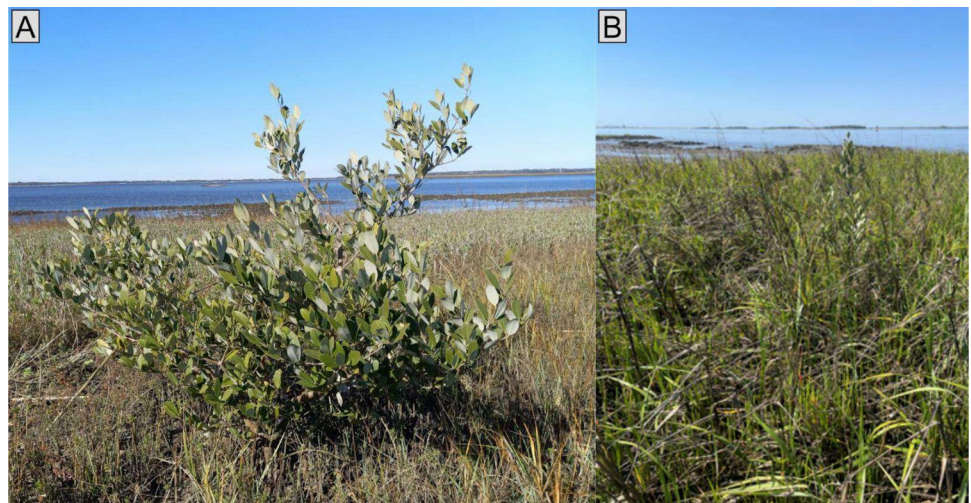


Fig. 4 Photographs of *Avicennia germinans* (black mangrove), individuals in early 2024 from Georgia, United States. Photo credits: **A** S.F. Jones, University of North Florida; **B** W.C. Vervaeke, National Park Service



near present-day Fernandina Beach, Florida (Muir 1919). At that time, Ponce Inlet, > 160 km to the south, was considered the northern limit of mangroves along the Atlantic coast of North America (Cavanaugh et al., 2019). Based on our recent observations and the 1867 historical data from Muir's book, we conclude that while mangroves were distributed further north than previously recognized in the past, there has been a rapid expansion of mangroves since the turn of the millennia (Cavanaugh et al., 2019; Osland et al., 2021, 2022; Snyder et al., 2022). To our knowledge, this is the first record of naturally occurring mangroves in Georgia.

Anthropogenic climate change has likely already altered the conditions that allow mangrove survival poleward up the coast of Georgia. Over the past 54 years, average winter temperatures in Jacksonville, Florida, and Savannah, Georgia,

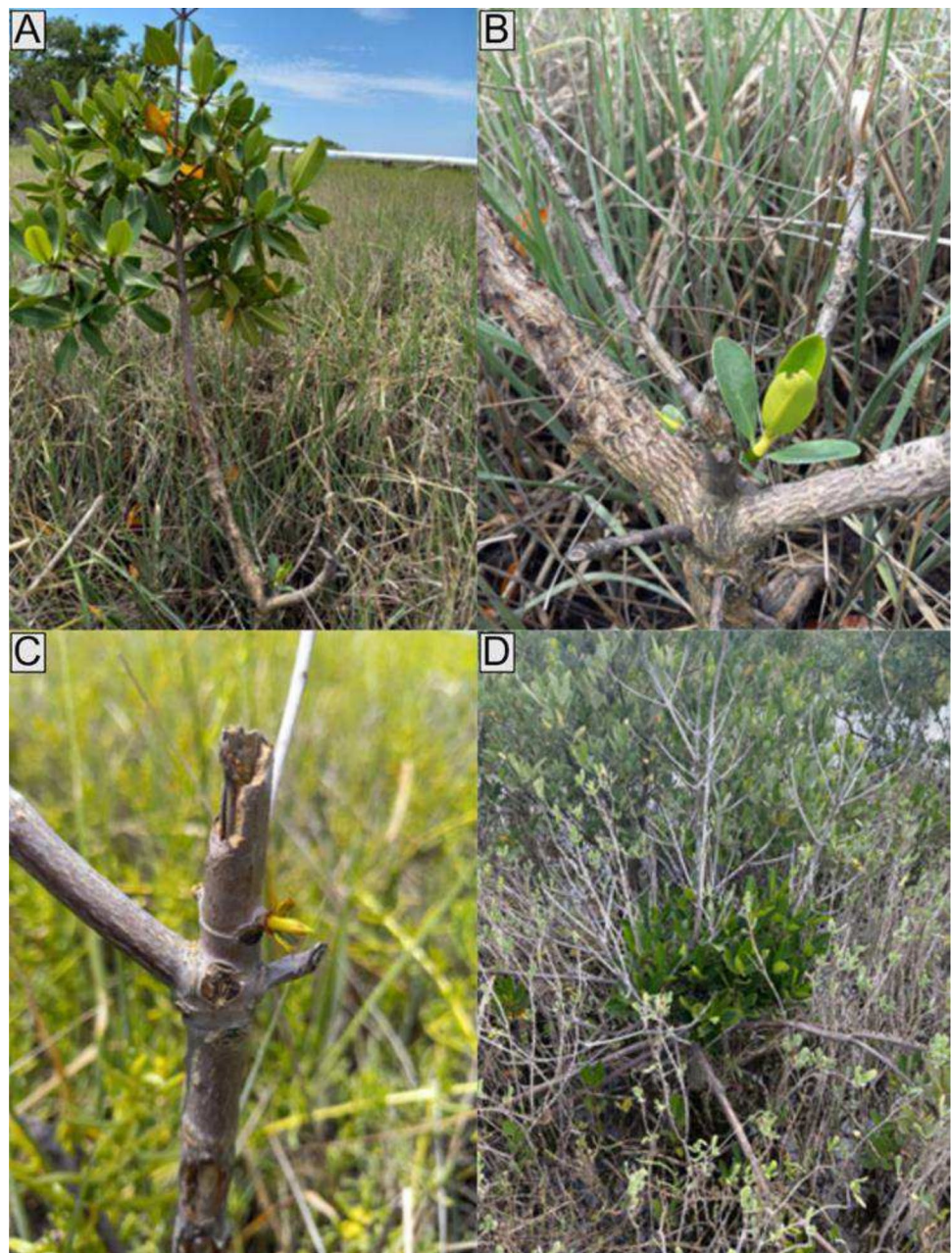
have risen 3.4 °C and 4.1 °C, respectively (<https://www.climatecentral.org/climate-matters/2023-winter-package>). The lowest officially recorded temperature in Jacksonville, Florida, for the last 10 years ranges between −4 °C in 2014 and −3 °C in 2023. The coldest temperature recorded for the last 25 years was −7 °C in 2013 (<https://www.currentresults.com/Yearly-Weather/USA/FL/Jacksonville/extreme-annual-jacksonville-low-temperature.php>), a temperature likely fatal to *A. germinans* (Osland et al., 2019). Surreptitiously planted *A. germinans* individuals have also survived at St. Simon's Island at 31.1408° N for ~15 to 20 years before removal, showing the possibility of mangroves establishing poleward (by over 42 km; Vervaeke pers. obs.) of current distributions. While regional patterns of freeze events may set the overall limit on mangrove survival, warmer water

and interactions with vegetation can influence local microclimate at small spatial scales, allowing conditions amenable for mangrove survival during seemingly lethal freeze events (Devaney et al., 2017; Osland et al., 2019).

Mangrove expansion is difficult to detect without intensive on-the-ground surveying, as temperature data alone cannot predict individual mangrove establishment and survival. Remote sensing can underestimate mangrove expansion due to patchy distributions within the marsh-mangrove ecotone, small stature, and rapid recruitment and change relative to image availability and resolution at higher latitudes (Jia et al., 2023). Newly available high-resolution imagery shows

promise for detecting mangroves at portions of the ecotone where in situ reproduction is leading to patch expansion, but seedlings' and young plants' small size and height below the marsh canopy during initial establishment make mangroves difficult to detect at mangrove's range limit (Doughty et al., 2024). Ground surveying has its constraints, such as appropriate tides and access to difficult-to-reach areas. A combination of regional imagery analyses coupled with ground surveys may therefore be the best practice for detecting and reporting expanding foundation species, especially in under-surveyed regions such as northeast Florida and southeast Georgia (Bardou et al., 2023).

Fig. 5 Photographs of *Rhizophora mangle* (red mangrove) individuals in 2024 exhibiting regrowth after freeze damage from late December 2022. **A** Individual showing one surviving stem and several dead stems, with regrowth at base of live main stem. **B** close-up photo of regrowth from individual in **A**. **C** Regrowth initiating from below stem that had been mortally damaged from freezing temperatures. **D** Basal regrowth of several shoots from individual that had appeared dead after initial freeze damage. Photo credits: **A–C** S.F. Jones, University of North Florida; **D** W.C. Vervaeke, National Park Service



The emerging pattern of mangrove distribution at the northern range limit in the southeastern United States has highlighted the distinct need for additional investigation into the eco-physiology of *R. mangle*. Despite lower intrinsic physiological tolerance to freeze events, *R. mangle* is currently distributed as far north as *A. germinans*, similar to patterns observed on the Florida Gulf Coast in Apalachicola Bay (Snyder et al., 2022). Temperature thresholds that lead to damage and mortality of *R. mangle* are less understood than those for *A. germinans*, but they are generally thought to be warmer (~ -4.5 °C for *R. mangle* mortality compared to -6.6 °C for *A. germinans*; Osland et al., 2021, Kang et al., 2024). These thresholds are approximate, as freeze duration can also play a role in mortality processes. Mangroves of both species found in Georgia, all estimated to be 3 years old or older, survived a freeze event on December 24, 2022, when a nearby NOAA Gauge (8,679,598) recorded a low temperature of -4.6 °C. This freeze event was nearly concurrent with high tide, potentially buffering the microclimate these mangroves experienced (Osland et al., 2019). Beyond open questions on the potential differences between the fundamental and realized physiological freeze tolerance of *R. mangle*, there is a need for basic physiological stress response research. Freeze-affected *A. germinans* individuals often show leaf browning when damaged and can exhibit epicormic growth in the recovery phase, leading to shrubby growth (Feller et al., 2023). Less is known about how *R. mangle* individuals respond to sub-lethal freeze damage. The northernmost *R. mangle* individuals demonstrate a distinct shrubby morphology that may be in response to freeze events, and the authors have observed regrowth from seemingly dead stems (Fig. 5), contrary to the prevailing understanding of *Rhizophora* physiology based on storm damage recovery and experimental pruning (e.g., Gill & Tomlinson, 1969, 1971).

Further investigations exploring the drivers controlling mangrove distribution and eco-physiology at the range limit will be important to predict future expansion. Surveys conducted on Amelia Island have found large numbers of *A. germinans* propagules stranded on the beach at Fort Clinch at the mouth of the St. Marys River after Hurricane Irma in 2017 (Kennedy et al., 2020); it is unclear if such stochastic storm events led to pulsed age cohorts of expanding mangroves. Resource managers with a desire to predict potential mangrove expansion may consider conducting post-storm beach surveys to quantify the number of propagules of both species available for recruitment. Hydrologic drivers disperse mangrove propagules and influence successful establishment after stranding (Balke et al., 2014, Yando et al., 2020). The regular semidiurnal tides along this coast may move *A. germinans* propagules around the lower marsh, whereas the elongated shape of *R. mangle* propagules may facilitate entrapment in the dominant low marsh *S.*

alterniflora (Goldberg & Heine, 2017). There is an urgent need for additional field surveys of mangrove distribution, field experiments testing *R. mangle* eco-physiology, and focused landscape analysis of potential dispersal pathways at the northern range limit of mangroves on the southeast Atlantic Coast of the United States. As these knowledge gaps are filled, coastal resource managers will have better predictions for when and where mangrove foundation species may expand into current saltmarsh habitats in the future. With this record and additional training, natural resource managers throughout coastal Georgia will be able to identify and report new mangrove individuals farther north than the ones described here as they expand their range.

Competing Interests

The authors declare no competing interests.

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Author Contribution WCV originally conceived and organized field trips. All authors contributed equally to the field explorations and writing of this manuscript.

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Data Availability The data supporting this study are available within the article.

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