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

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Abstract

Ongoing 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 farther north than they would have in the past. A well-studied example of this tropicalization is the expansion of mangroves at the marsh-mangrove ecotone, thought to be controlled by a decrease in extreme freeze events in the SE USA. However, accurate mangrove distribution data at their poleward limit in this region is currently lacking. Here, we report information collected from targeted surveys along the Atlantic coasts of Florida and Georgia at the poleward limit of mangroves in the USA. We document both *Avicennia germinans* and *Rhizophora mangle* individuals naturally occuring in Georgia, USA, poleward of previous reports by more than 23 km (*A. germinans*) and by almost 80 km (*R. mangle*), respectively. 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 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 needed insight as current landscapes change.

Introduction

Climate change is altering environmental conditions and causing range shifts of foundation species, including through the tropicalization of temperate areas (Bates et al. 2014, Osland et al. 2021, McLean et al. 2021). Tropicalization, caused by decreases in the frequency of extreme cold events, may be 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 species change when conditions shift (Osland et al. 2023). Subtropical saltmarshes in the SE USA, for example, are expected to experience mangrove expansion as a result of tropicalization, which could profoundly affect coastal ecosystem structure and function (Cavanaugh et al.2019, Chapman et al 2021, Osland et al. 2022). In contrast, other regions especially 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).

In the SE USA, where increased minimum temperatures are likely driving mangrove expansion, climate projection models suggest a 5°C increase in annual temperature minimums, potentially allowing mangrove distribution to expand as far north as South Carolina, USA (Cavanaugh et al. 2019). This region also has a strong research base exploring the functional implications and drivers of ecotonal shifts with climate change (Rodriguez et al. 2016, Simpson et al. 2017, Osland et al. 2019). Due to rapidly changing environmental conditions and potential shifts in ecosystem function across an area with large expanses of saltmarsh habitat (Worthington et al. 2023), a regional approach to tracking species range shifts may be most useful, as demonstrated for expanding mangroves in Apalachicola Bay, 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 NE 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; the region is known to be undersampled (Bardou et al. 2023). Currently, the northernmost published mangrove location (*Avicennia germinans*), is at Fort George Inlet in the Timucuan Ecological and Historic Preserve in Jacksonville, FL USA (Cavanaugh et al. 2019) with the northernmost individual on the southern tip of Amelia Island (Kennedy et al. 2020). The northernmost reported *R. mangle* is in the Guana Tolomato Matanzas National Estuarine Research Reserve (Frazel 2009). However, despite these records, there remains a distinct data gap on the current distribution of the northernmost mangroves on FL's Atlantic coast (Bardou et al. 2023), which are the northernmost mangroves in the USA.

This gap is hindering prediction of future mangrove expansion and the ecological effects of foundation species turnover. Here, we detail the results of field surveys aimed at filling mangrove distribution gaps at their range limit in NE FL, conducted in 2024. We report both black mangrove (*A. germinans*) and red mangrove (*R. mangle*) as naturally-occurring in Georgia, USA, at latitudes > 30.72 °N.

Materials and Methods

Site setting

The northern range limit of mangroves in the SE USA currently occurs near the Florida-Georgia border. This border follows the St. Mary's 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, FL southward) to riverine estuaries with back-barrier complexes (Jacksonville, FL northward) (Dame et al. 2000). Marshes in the region are typically dominated by *Spartina alterniflora* in the low marsh, with *Juncus romerianus* in the high marsh and in areas with brackish salinities (Odum 1988, Dame et al. 2000). 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 FL, 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; some of the largest tides in the SE USA. The climate in this region is humid subtropical (Köppen Cfa; Beck et al. 2018) with the lowest average monthly temperature 8.7°C and highest 32.3°C (usclimatedata.com). The region sees frequent tropical storm systems, and although initial direct hits are rare has had 8 storms track within 100 km over the last 10 years, (noaa.gov).

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. Surveys in January and February 2024 were conducted between the Nassau River, FL, and St. Mary's River along the ICW (Fig. 1). Both surveys expanded to the north side of the St. Mary's 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 May 2024 to confirm locations and collect additional data on the northernmost mangroves in FL (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 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 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 GA, USA, with an *R. mangle* individual 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, FL (Vervaeke, unpub. data). Northernmost mangrove individuals were generally small and young (Figs. 3–4, Table 1). All *R. mangle* individuals reported here were shorter than 0.75 m tall 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 five years old.

Table 1
Location, elevation, and plant structural data for all currently-known mangroves in Georgia and the northernmost mangroves in Florida, USA.

Location	Species ID	Location (lat, long)	Elevation (m NAVD88)	Height (m)	Diameter (m)	Age (years)	Reproductive status
Georgia, USA							
	R. mangle	30.73529, -81.49527	0.798	0.74	0.40, 0.33	4	Y(flowers and fruit)
	R. mangle	30.73479, -81.49554	0.889	0.57	0.29, 0.28	3	Y(flowers)
	R. mangle	30.73471, -81.49557	0.876	0.45	0.23,0.19	3	N
	R. mangle	30.73438, -81.49561	0.754	0.69	0.58,0.44	4	N
	A. germinans	30.73139, -81.50038	0.693	0.80	0.46, 0.34	4	N
	A. germinans	30.73152, -81.48027	0.717	0.76	0.30, 0.22	3	N
	A. germinans	30.73030, -81.50053	0.809	1.33	1.66, 1.49	5 to 7	Y (propagules)
Florida, USA							
	R. mangle	30.68624, -81.46477	0.624	0.70	0.31, 0.28	3	N
	A. germinans	30.67149, -81.47694	0.799	0.70	1.55, 1.48	> 5	Y(flowers)

Discussion

Our report of naturally-recruited *A. germinans* and *R. mangle* individuals in GA provides evidence that mangroves may be establishing poleward of their historical range limits in the SE USA. 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). Periods of warming followed by periodic freeze events are natural and expected to continue (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 near present-day Fernandina Beach, FL (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 in the past mangroves were distributed further north than previously recognized, 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).

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, FL, and Savannah, GA have risen 3.4°C and 4.1°C, respectively (Climate Central). The lowest officially recorded temperature in Jacksonville, FL 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 (Current Results), a temperature likely fatal to *A. germinans* (Osland et al. 2019). Surreptitiously planted *A. germinans* individuals have also been identified growing at St Simon's Island at 31.1408°N, north of the mangroves described here by over 42 km (Vervaeke personal observation). While they are no longer extant, these mangroves survived for ~ 15 to 20 years, showing the possibility of mangroves establishing poleward of current distributions.

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 ecotone, but small size and height below the marsh canopy during initial establishment make mangroves difficult to detect (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 NE Florida and SE Georgia (Bardou et al. 2023).

The emerging pattern of mangrove distribution from the northern range limit in the SE USA has highlighted the distinct need for additional investigation into the eco-physiology of *R. mangle*. Despite lower inherent physiological tolerance to freeze events (Kang et al. 2024), R. *mangle* is currently distributed as far north as *A. germinans*, similar to patterns observed on the FL 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. 2020, Kang et al. 2024). Mangroves of both species found in GA, all estimated to be three years old or older, survived a freeze event on December 24, 2022, when a nearby NOAA Gauge (8679598) 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 fundamental physiological freeze tolerance and realized 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 show 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 and 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 Mary's 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. Post-storm surveys could be conducted at the northern range limit 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. 2015, 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 *Spartina alterniflora* (Goldberg and 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 SE Atlantic Coast of the USA.

Declarations

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Figures

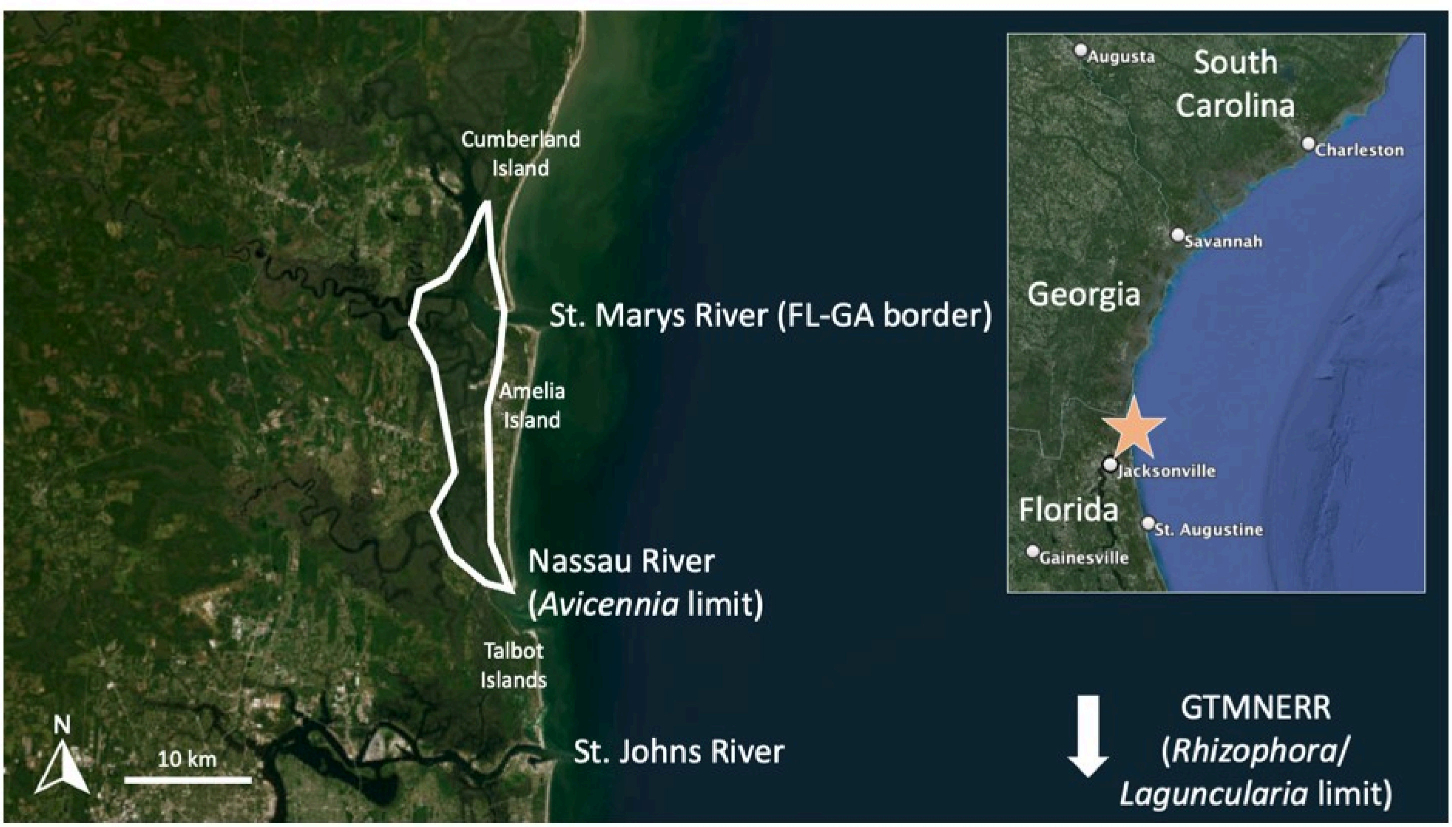

Figure 1

Map of the region under study with specific survey areas in Florida and Georgia, USA, and current northern distributional limits of mangrove species reported in the literature.

Figure 2

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

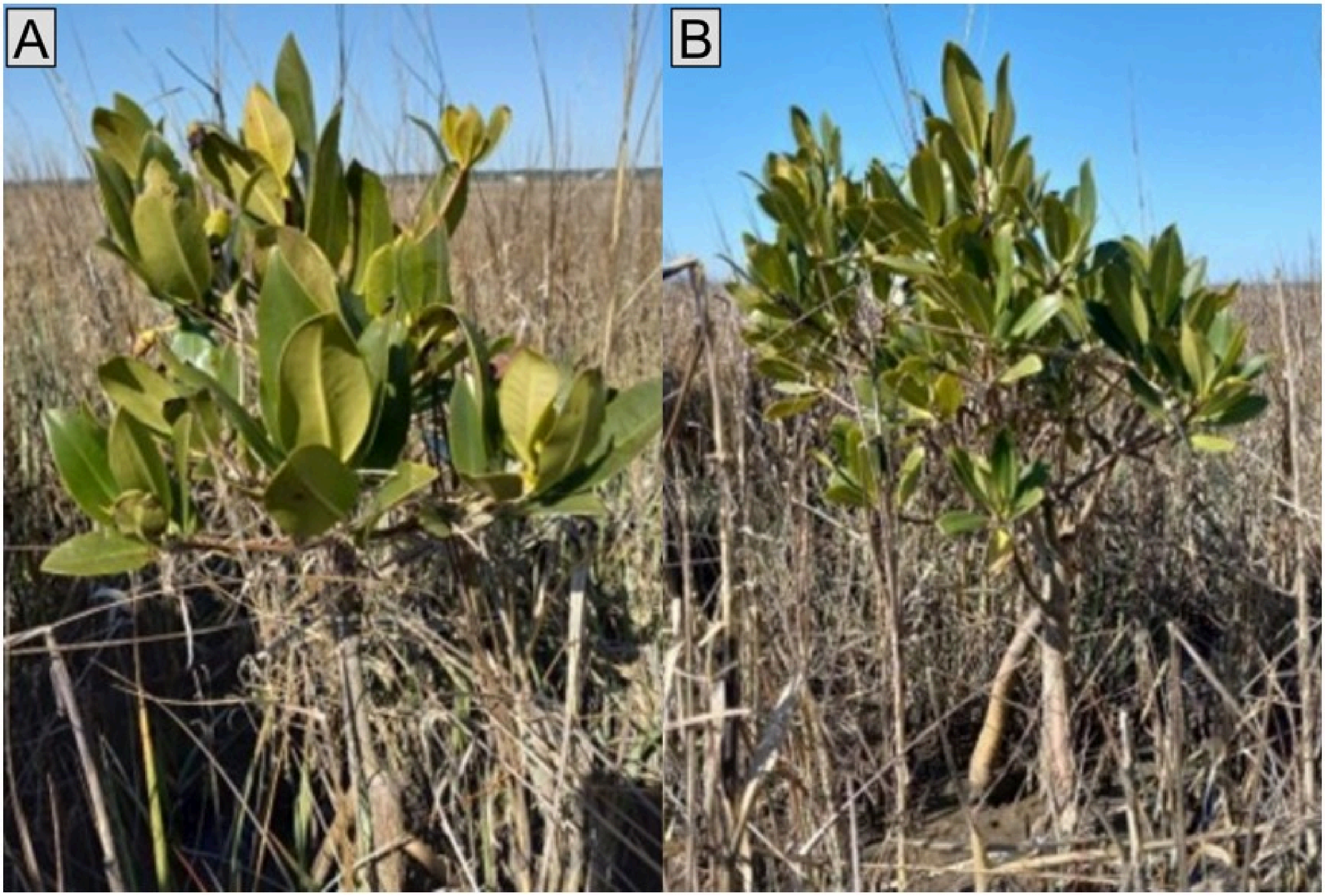

Figure 3

Photographs of red mangrove, *Rhizophora mangle*, individuals in early 2024 from Georgia, USA. Photo credits: A-B S.F. Jones, University of North Florida.

Figure 4

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

Figure 5

Photographs of red mangrove, *Rhizophora mangle*, 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.